The ammonite zonal sequence and ammonite taxonomy in the *Douvilleiceras mammillatum* Superzone (Lower Albian) in Europe

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Synopsis

The Lower Albian Substage is divided into an earlier Zone of *Leymeriella tardefurcata* and a later Zone of *Douvilleiceras mammillatum* the biostratigraphy of which is the subject of the present paper. Although the epicontinental seas of Europe encompassed a single ammonite faunal province during the *mammillatum* Zone, sedimentary sequences are scattered and incomplete in their subzonal representation. As a consequence, different zonal and subzonal schemes have been devised for the relatively well known and well developed sequences in England, France, and the Soviet Union. Four such schemes are in current use, all reflecting the degree of representation in the particular region concerned. Because of this variation in the degree of representation in the *mammillatum* Zone lithological sequences, disagreement has arisen between French and English workers on the status and position of the Subzones of *Otohoplites raulinianus* and *Protohoplites* (*Hemisonneratia*) *puzosianus*. This disagreement has important implications both from the stratigraphic point of view and for the ammonite systematics. Sufficient information is available to settle this problem and to correlate the zonal and subzonal schemes currently in use in the Soviet Union with that of western Europe. A revised zonal and subzonal scheme is established in this paper which can be applied to the whole of the European province in the later part of the Lower Albian; the rank of the Zone of *Douvilleiceras mammillatum* being raised to that of a Superzone with global application during this period of time.

A review of the ammonite fauna is made. On the basis of new evidence, the Cleoniceratidae is redefined as a family with three subfamilies, the Vnigriceratinae, the nominate subfamily Cleoniceratinae, and the Lemuroceratinae nov. The Hoplitidae is considered to consist of three subfamilies, the Hoplitinae *sensu stricto*, the Sonneratiinae, and with some question the Gastroplitinae. A number of species of individual genera, described separately from western and eastern Europe, are considered to be conspecific.

Introduction

Lower Albian sediments in Europe are very scattered in occurrence, frequently condensed and incomplete in their representation of the subzonal sequence, and there is much evidence of periods of strong current-scour activity reflecting relatively shallow epicontinental seas in which tectonic movements were manifest. Only in relatively deep basins are thick and more continuous sedimentary sequences preserved. Elsewhere, the periods of submarine current-scour reduced previous episodes of sedimentation to remnants, or to phosphatic pebble horizons which may, in turn, have been reworked more than once. This latter feature of polyphase erosion has produced difficulties in the determination of the ammonite subzonal sequence, and even of the zonal sequence, when mixtures of disinterred *Leymeriella tardefurcata* Zone and *Douvilleiceras mammillatum* Superzone pebble faunas have occurred. This is well illustrated by the condensed phosphatic pebble bed sequences in the northern alpine zone extending from the Alpes Maritimes (France) eastwards through Switzerland, Austria and southern Germany. Even in the relatively deep basinal areas such as the Harz foredeep region in the *tardefurcata* Zone and the central Aube and northern Pays de Bray in the *mammillatum* Superzone, non-sequences or periods of strong current-induced condensation are to be found. There is borehole evidence of a relatively thick development of clays of later *mammillatum* Superzone age in the Harz foredeep in the Hannover-Braunschweig area of north Germany, a development which might also be present in the Polish Trough. Elsewhere at outcrop in north Germany and Poland, strong current scour has condensed or removed altogether sediments of this Superzone.

In the case of the *Douvilleiceras mammillatum* Superzone, these episodes of non-sequence and erosional condensation have led to a disagreement in western Europe concerning the sequence of Subzones and the zonal scheme. Furthermore, in the Soviet Union, thick *mammillatum* Superzone sequences are present in the Mangyschlak Peninsula, Transcaspia, in which a different zonal scheme from that of western Europe has been recognized, albeit that the ammonite faunas are closely comparable. Although parts of the sequence are better developed than in contemporaneous sediments in western Europe, non-sequences are apparent also in Mangyschlak. Nonetheless, the ammonites figured so far permit a direct correlation of the Russian zonal scheme with that of England and France.

The intention of this paper is to discuss the evidence of ammonite faunal succession within the *mammillatum* Superzone in Europe in order to stabilize a zonal and subzonal scheme which can be applied throughout the whole of this ammonite faunal province. Although the ammonite fauna contains elements which are more geographically widespread than the epicontinental seas of Europe, such as *Douvilleiceras*, *Beudanticeras*, *Cleoniceras*, *Tegoceras*, *Oxytropidoceras*, *Protanisoceras*, *Rossalites* and *Hamites*, ammonites such as *Sonneratia* and *Pseudosonneratia*, together with their offshoots *Otohoplites*, *Protohoplites*, *Tetrahoplites* etc., are restricted to the European shelf seas. In this respect, the distribution of this latter restricted group of ammonites within the *mammillatum* Superzone European faunal province presages the hoplitinid faunal province recognized in the Middle and Upper Albian, and which continues into the Cenomanian.

Current zonal and subzonal schemes

Prior to 1984, two fundamentally different zonal and subzonal schemes were in use for western European *mammillatum* Superzone sequences. The first of these schemes was erected by Casey (1961) and has been used throughout his important monograph of the Lower Greensand Ammonoidea (Casey 1960–) and by other workers in the United Kingdom. The second scheme was devised by Destombes (1973, 1979) based upon sequences exposed in northern France. A variation of this latter scheme has been proposed by Amédro (1980, 1981, 1984*a*, *b*).

In the Soviet Union, Savel'ev (1973*a*, *b*, 1974) has made a detailed study of the Lower Albian sequence in the Mangyschlak Peninsula, Transcaspia. Based on this sequence, he has erected an apparently distinct zonal and subzonal scheme from that recognized in the *mammillatum* Superzone of western Europe. However, his Subzones can be correlated directly with those of western Europe because most of the distinctive species are present in the sequences at both extremities of the European province. These different schemes are discussed now in greater detail.

Casey (1961)

Careful bed by bed collecting in the Gault–Lower Greensand Junction Beds in southern England and East Anglia allowed Casey (1961) to revise the ammonite subzonal sequence of the *Douvilleiceras mammillatum* Zone of earlier workers such as Spath (1923–43). He divided the Zone into four Subzones as shown in Table 1.

Stratigraphic basis of the scheme

The lithological representation of the *mammillatum* Zone in southern England and in East Anglia was recognized as being marked by episodes of current induced condensation and non-sequence which involved different time intervals at different places. No single section has yet revealed a continuous and relatively complete lithological succession in which the full sequence of ammonites can be demonstrated. However, there are sufficient sections available in which the sequence of Subzones can be determined without doubt. The ammonite fauna of these sediments has been described and illustrated by Casey (1960–) together with the stratigraphy based on key sections (Casey 1961).

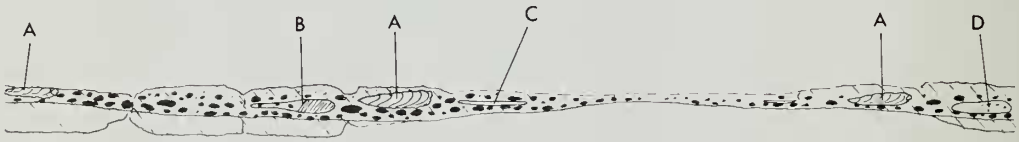
Table 1 Subzonal schemes of the *mammillatum* Zone according to Casey (1961).

Substage	Zone	Subzone
Middle Albian (part)	*Hoplites dentatus* (part)	*Hoplites (Isohoplites) eodentatus*
Lower Albian	***Douvilleiceras mammillatum***	***Protohoplites (Hemisonneratia) puzosianus***
		Otohoplites raulinianus
		Cleoniceras floridum
		Sonneratia kitchini
	Leymeriella tardefurcata	*Leymeriella regularis*

The earliest Subzone in his scheme is characterized by *Sonneratia kitchini* Spath. It is represented by sediments in the region of West Dereham, Norfolk, in Casey's view, where its relationship to the earlier *Leymeriella regularis* Subzone (*tardefurcata* Zone) and the later *Cleoniceras floridum* Subzone is not established (Casey 1961, 571). In the Leighton Buzzard district, Bedfordshire, the *kitchini* Subzone ammonite fauna is mixed with that of the *regularis* and *floridum* Subzones (Casey 1961, 567–8; Owen 1972). In the Squerryes Estate sandpit at Westerham, the *kitchini* Subzone fauna is seen to occur below that of the *floridum* Subzone (Casey 1961, 543). At Folkestone, Kent, the thin *kitchini* Subzone nodule bed occurs above sediments of reported *regularis* Subzone age and beneath the mixed *floridum* and *raulinianus* Subzones fauna of the phosphatic pebble debris in Bed 1a (Casey's Bed 33; 1961, 528–30). In the Isle of Wight, the *kitchini* Subzone is represented within the Carstone Member of the Lower Greensand.

This brief review serves to illustrate the fact that *kitchini* Subzone sediments are very widely scattered in occurrence in England. Moreover, when compared with the sequence in the Mangyschlak Peninsula in the Soviet Union, mentioned below, in which two distinct Subzones have been recognized, it is clear that the English sequence is very imperfect. Yet, there is evidence that both the Subzones recognized in the Soviet Union can be detected also in England (pp. 198–201).

Sediments of *floridum* Subzone age are of widespread occurrence in southern England. The sections in which they are known to be most fully developed at present are the Squerryes Estate sandpit near Westerham, Kent (Casey 1961, 543) and the Coney Hill sandpit near Barrowgreen House, Tandridge, Surrey (Wright & Wright 1948). In the Squerryes sandpit, the relationship between the earlier *kitchini* Subzone sediments is clearly established, but the relationship with the *raulinianus* Subzone fauna is not. At Ford Place, near Trottiscliffe, Kent, ammonites of the *floridum* Subzone occur in the lower part of the Gault–Lower Greensand Junction Beds (Casey 1961, 545–6). They are separated from sediments of undoubted *puzosianus* Subzone age by a thin sequence (Beds 5 and 6 of Casey) which Casey classified with the *raulinianus* Subzone and which have yielded *Otohoplites raulinianus* (d'Orbigny). At Folkestone, the single concentration of phosphatic nodules in Bed 1a (Bed 33 of Casey 1961, 528–30) contains *en melée* phosphatized pebble ammonite fragments indicating debris derived from both the *floridum* and *raulinianus* Subzones former sediments. The matrix in which this phosphatic debris is embedded contains partly crushed, partly phosphatized ammonites of *puzosianus* Subzone age (Fig. 1). As the nodules are to be found in the remains of the crushed ammonite body chambers as well as



LEGEND

Phosphatic pebbles, mainly fragmentary casts of fossils derived from former deposits of the *floridum* and *raulinianus* Subzones, buff coloured when fresh turning black when exposed to sea-water, embedded in a shelly, grey, pebbly and clayey grit, weathering to yellow.

A. Large *Exogyra latissima* and *Gryphaeostrea canaliculata*

B – part phosphatised, C – totally crushed, and D – partly crushed unphosphatised sandstone casts of indigenous *puzosianus* Subzone ammonites with traces of the shell.

Secondary concretionary induration.

Fig. 1 Diagrammatic section through Bed 33 of Casey (1961), Gault–Lower Greensand Junction Beds, Copt Point, Folkestone, Kent.

above and below them, the *raulinianus* Subzone element of the pebble fauna is earlier than the *puzosianus* Subzone, not later as advocated by Destombes (1979) and Amédro (1980). A selection of ammonites from the indigenous fauna of this bed is illustrated in Figs 2–11 and Fig. 36.

Sediments of *puzosianus* Subzone age are of widespread occurrence in the sections around the northern margins of the Weald from Folkestone, Kent, to Farnham, Surrey. However, there is usually a thickness of sediment separating known beds of *puzosianus* Subzone age from beds containing '*Hoplites* (*Isohoplites*) *eodentatus*' Casey taken by him, and all subsequent workers until 1984, to mark the base of the Middle Albian Substage and the Zone of *Hoplites dentatus*. In order to provide an index ammonite which was far more cosmopolitan in distribution to mark the base of the Middle Albian Substage, it was agreed at the Copenhagen meeting on Cretaceous Stage and Substage boundaries, held in 1983, to place the base of the Middle Albian Substage at the appearance of *Lyelliceras lyelli* (Leymerie) (Owen 1984). The '*eodentatus*' Subzone sediments rest directly upon sediments of *puzosianus* Subzone age at Folkestone and at Sandling Junction, Kent. However, work in France convinced the writer that an important non-sequence existed in England between the *puzosianus* and '*eodentatus*' Subzones involving the *Otohoplites bulliensis* Subzone of Destombes, discussed below (Owen 1976, 1985). Although not proven, it is likely that the sedimentary interval between the *puzosianus* and '*eodentatus*' Subzones sediments seen in north-west Kent and Surrey is of *bulliensis* Subzone age.

In summary, it is readily apparent that the ammonite subzonal sequence recognized by Casey in England is well based despite the isolated, or strongly condensed, nature of the thin sediments representing the various Subzones. Equally it is clear, from much fuller developed sequences elsewhere in Europe, that other Subzones are present which are poorly represented or have yet to be identified positively in England.

Destombes (1973, 1979)

The equally careful collecting from well developed *mammillatum* Superzone sequences in the Aube and Pays de Bray regions of France by P. and J.-P. Destombes over a period of many years has led P. Destombes to disagree with the zonal and subzonal scheme proposed by Casey. Destombes' scheme is radically different from that of Casey and is set out here in Table 2. In 1973, Destombes recognized a Subzone of *Otohoplites normanniae* above that of *O. bulliensis*, but this is omitted in his scheme of 1979.

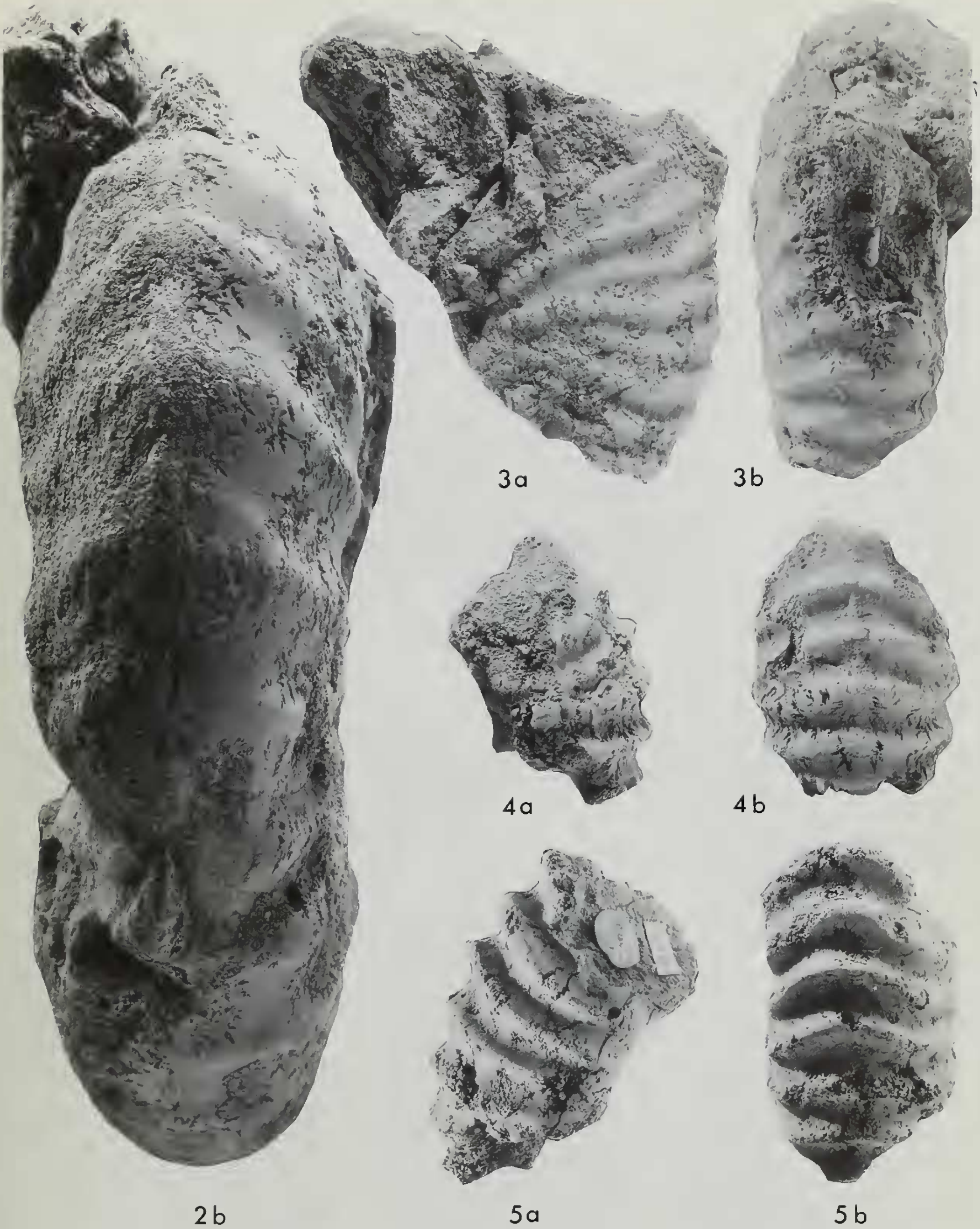
The scheme proposed by Destombes (1979) illustrates an important fact; that the earlier part of the *mammillatum* Superzone is characterized by *Sonneratia* and the later part by *Otohoplites*. However, his scheme fails to reflect accurately the known ammonite sequence. Sections in Kent show that the *puzosianus* Subzone, which contains species of *Otohoplites*, does not follow directly upon that of *Cleoniceras floridum* as advocated by Destombes, but is separated from it by an interval (Casey's *raulinianus* Subzone) which contains *Otohoplites raulinianus* and closely related forms. The index ammonite *Sonneratia dutempleana* is restricted to the *puzosianus*

Table 2 Zones and Subzones of the *Douvilleiceras mammillatum* Superzone according to Destombes (1979).

	Zone	Subzone
	Hoplites dentatus (Middle Albian)	*Isohoplites eodentatus*
Douvilleiceras mammillatum	***Otohoplites raulinianus***	***Otohoplites bulliensis*** ***Otohoplites larcheri***
	Sonneratia dutempleana	***Protohoplites (Hemisonneratia) puzosianus*** ***Cleoniceras (Cleonella) floridum*** ***Sonneratia kitchini***
	Leymeriella tardefurcata	*Leymeriella regularis*

2a

Fig. 2a *Pseudosonneratia* (*Isohoplites*) *occidentalis* Casey. Indigenous *puzosianus* Subzone fauna of Bed 33, Gault–Lower Greensand Junction Beds, foreshore reefs near Copt Point, Folkestone, Kent. BMNH C90175 Author's Coll. × 1.



Figs 2b–5 Ammonites from the partly crushed indigenous fauna of *puzosianus* Subzone age of Bed 33, Gault–Lower Greensand Junction Beds, foreshore reefs near Copt Point, Folkestone, Kent. Author's Coll. all × 1.

Fig. 2b *Pseudosonneratia occidentalis* Casey BMNH C90175, peripheral view of the specimen figured in Fig. 2a.

Figs 3a, b *P.* (*I.*) *occidentalis* Casey BMNH C69872.

Figs 4a, b *Tetrahoplites* sp. BMNH C69873.

Figs 5a, b *Pseudosonneratia* (*Pseudosonneratia*) *typica* Spath BMNH C72259.

Subzone and is atypical of the species of *Sonneratia* occurring in the earlier part of the *mammillatum* Superzone included by Savel'ev (see below pp. 191, 219) in the subgenera *Globosonneratia* and '*Eosonneratia*'. The stratigraphic basis of Destombes' scheme is set out below and he has provided the evidence by which it can be tested.

Stratigraphic basis of the scheme

In France, *mammillatum* Zone sediments are preserved in three distinct facies. In the Boulonnais and in the Argonne, the sediments and the mode of condensation are much the same as at the outcrop in east Kent in England, with condensed phosphatic pebble faunas and major non-sequences. In the northern Pays de Bray and around the southern part of the Paris Basin in the ancient district of Perchois, relatively thick clays and glauconitic loams are present. Elsewhere in southern France and in the Pays de Caux, Normandy, polyphase erosion has produced mixed faunas and strongly condensed sequences. Even in the well developed sedimentary sequences in the Aube and Pays de Bray, the subzonal representation is incomplete.

There is no certain evidence of the presence of uncondensed sediments of *Sonneratia kitchini* Subzone age, in Casey's sense, in France. The possibility that the basal part of the Argiles Tegulines in the south-eastern Aube and in the Yonne are of *kitchini* Subzone age is attractive, albeit uncertain, in the absence of ammonite evidence (Destombes 1979, 123). In the mixed late-*tardefurcata* and early-*mammillatum* Zone faunas at Machéroménil (Ardennes), the *kitchini* Subzone is definitely represented. Ammonites of this Subzone are known also from the Perte-du-Rhône (Ain), but have not yet been found in the Alpes Maritimes.

Deposits of *Cleoniceras floridum* Subzone age are well developed in the region of the Bois du Perchois, Aube. The section in the Perchois Ouest quarry and its superb ammonite fauna have been described by Destombes (1979). The fauna is preserved in cementstone nodules and has been regarded as wholly indigenous to the encasing sediment (Bed 1b). On the other hand, at Wissant in the Boulonnais, Destombes' horizon P 1 (Destombes & Destombes 1965, Amédro 1981) contains *Cleoniceras floridum* Casey and other fossils as incomplete phosphatic pebbles remarkably similar in preservation to those in Casey's Bed 33 at Folkestone some 36 km away. No other occurrences of *floridum* Subzone sediments have been discovered in France outside of these two regions.

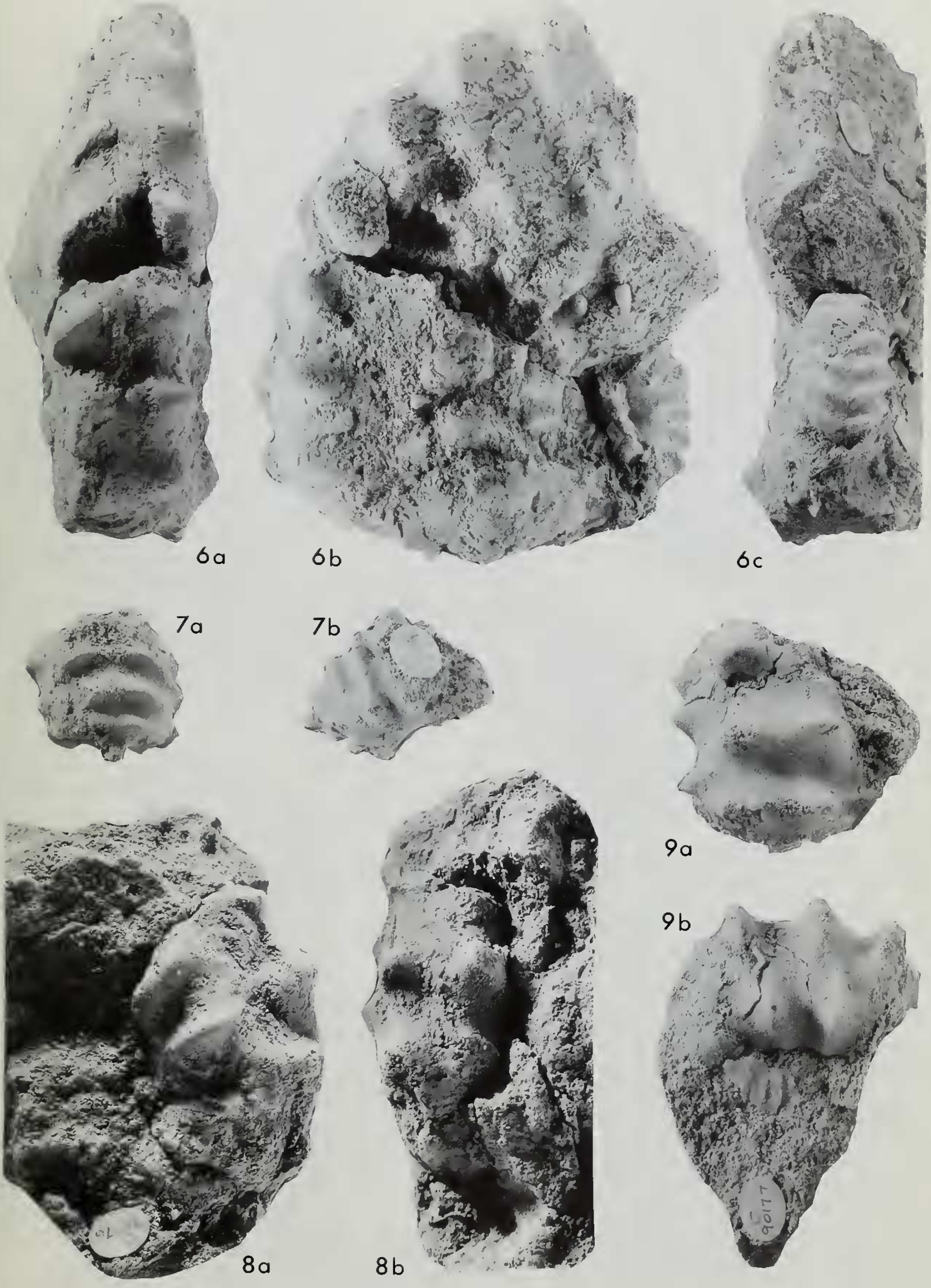
Above the *floridum* Subzone sediments (Bed 1b) of the Perchois Ouest quarry, Destombes discovered ammonite nuclei within his Bed 1c which he identified as *Protohoplites* (*Hemisonneratia*) *gallicus* Breistroffer of *puzosianus* Subzone age (Destombes 1979, 56). On the basis of this occurrence and the alleged presence of *Protohoplites* (*Hemisonneratia*) aff. *puzosianus* (d'Orbigny) in Bed 2b of the stratigraphically higher Perchois Est quarry, he concluded that the *puzosianus* Subzone follows directly upon that of *Cleoniceras floridum* and precedes his Subzone of *Otohoplites larcheri* represented in Bed 2b of the Perchois Est quarry. The specimens identified as *P.* (*H.*) *gallicus*, or compared with that species, and figured by Destombes are re-figured here in natural size. They are compared with the inner whorls of comparable species of *Sonneratia*, *Protohoplites* (*Hemisonneratia*) and of robust, simple ribbed, early forms of *Otohoplites* (p. 222, Figs 6c, 45–55). In the writer's opinion, these nuclei figured by Destombes (1979) are not strictly determinable at subgeneric or specific level. They do not provide evidence of the presence of the *puzosianus* Subzone in the sense of Casey (1961). The specimen from Bed 2b (*larcheri* Subzone) of the Perchois Est quarry identified and figured as *Protohoplites* (*Hemisonneratia*) aff. *puzosianus* (d'Orbigny) by Destombes (1979, pl. 4–18, fig. 3) appears to be a fragment of *Sonneratia*.

Figs. 6–9 Ammonites from the partly crushed indigenous fauna of *puzosianus* Subzone age of Bed 33, Gault–Lower Greensand Junction Beds, foreshore reefs near Copt Point, Folkestone, Kent. Author's Coll. all × 1.

Figs 6a–c *Protohoplites* (*Hemisonneratia*) aff. *puzosianus* (d'Orbigny) BMNH C69871.

Figs 7a, b *Protohoplites* (*Hemisonneratia*) *gallicus* Breistroffer BMNH C90179.

Figs 8a, b, 9a, b *Protohoplites* (*Protohoplites*) *archiacianus* (d'Orbigny) BMNH C90176 and C90177 respectively.


6a
6b
6c
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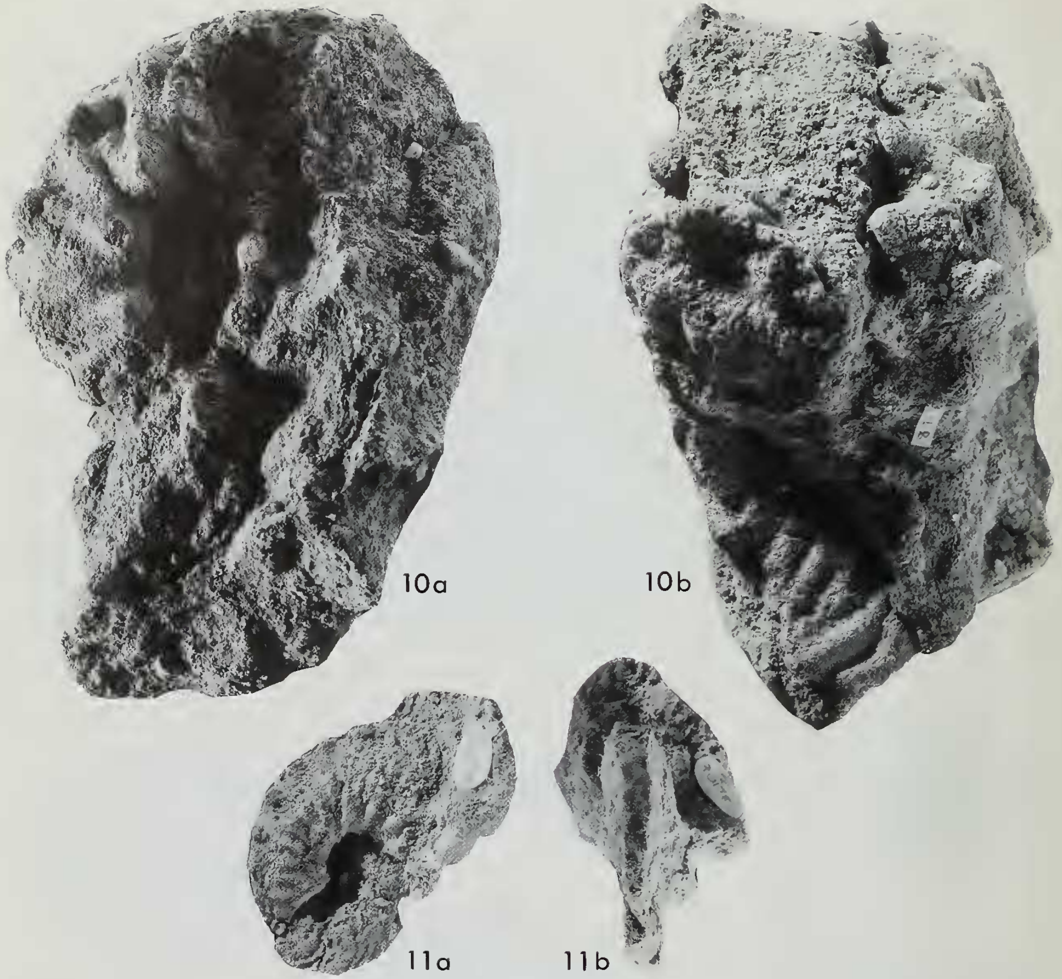

Figs 10–11 Ammonites from the partly crushed indigenous fauna of *puzosianus* Subzone age of Bed 33, Gault–Lower Greensand Junction Beds, foreshore reefs near Copt Point, Folkestone, Kent. Author's Coll. all × 1.
Figs 10a, b *Otohoplites destombesi* Casey BMNH C69870.
Figs 11a, b *Otohoplites* cf. *subhilli* (Spath) BMNH C90178a.

The species of *Otohoplites* from Bed 2b of the Perchois Est quarry described under the trivial name *larcheri* by Destombes (1979, 98; pls 4–18, fig. 4 and 4–22, figs 1–3) includes two species as understood by Casey. The paratype of *O. larcheri* figured by Destombes (1979, pl. 4–22, figs 1a, b) and reproduced here in Figs 12a, b, falls within the range of morphological variation shown by *Otohoplites raulinianus* (d'Orbigny). It is closely comparable to the early form of that species from the *raulinianus* Subzone figured by Casey (1965, 943; pl. LXXXIV, fig. 1) which is refigured here in Figs 13a, b. The holotype of *O. larcheri* figured by Destombes (1979, pl. 4–22,

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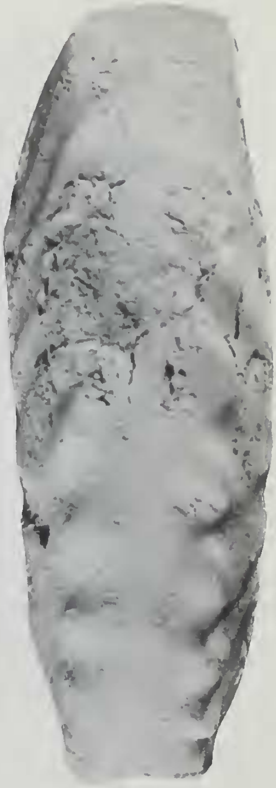
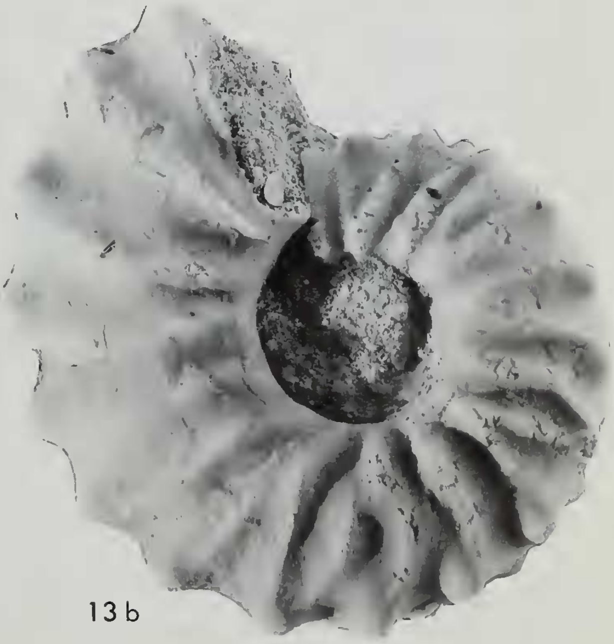
Figs 12, 13 *Otohoplites raulinianus* (d'Orbigny) both × 1.
Figs 12a, b Copy of Destombes' (1979, pl. 4–22, figs 1a, b) illustrations of a paratype of *Otohoplites larcheri*, Bed 2b, Perchois Est quarry, Aube, Destombes Coll. No. 18E.
Figs 13a, b A typical *raulinianus* Subzone form (partly figured by Casey 1960–, pl. LXXXIV, fig. 1 in side view only), Bed 33 phosphatic debris, foreshore reefs near Copt Point, Folkestone, Kent. British Geological Survey (BGS) GSM 70474 R. Casey Coll.

12a



12b

13a



13b

figs 2a, b) and the remaining paratype (pl. 4–18, fig. 4 and pl. 4–22, fig. 3) fall within the range of variation of *Otohoplites waltoni* Casey. Destombes' paratype from Perchois, and the holotype of *O. waltoni* figured by Casey (1965, pl. LXXXIII, figs 7a, b) from the condensed *floridum* and *raulinianus* Subzones debris in Bed 1a at Folkestone, are re-figured here in Figs 14a, b and 15a, b. Although *O. raulinianus* and *O. waltoni* range up into the *puzosianus* Subzone, they are a relatively subordinate element among the later species of *Otohoplites* and among species of *Protohoplites* (*Protohoplites*) and *P.* (*Hemisonneratia*). The *larcheri* Subzone of Destombes does not contain the typical fauna of the *puzosianus* Subzone and, bearing in mind the evidence of superposition of the *puzosianus* Subzone above the *raulinianus* Subzone in Kent, the *larcheri* Subzone of Destombes and the *raulinianus* Subzone of Casey are identical concepts of a single unit of relative time.

The *puzosianus* Subzone, in Casey's sense, is represented by condensed phosphatic pebble deposits in France at Wissant, Boulonnais (Owen 1971, 82–83), and at Machéroménil and Faissault in the Ardennes (e.g. Casey 1960–, parts VI and VII; Amédro & Destombes 1975). At all three localities, the typical fauna of the Subzone (see Table 6, pp. 208–11) is well represented. However, as at Sandling Junction in east Kent (Casey 1961), there are non-sequences above and below the *puzosianus* Subzone phosphatic nodule beds at Machéroménil and Faissault. At Wissant, the *puzosianus* Subzone nodule bed (Bed 7 of Owen 1971, 82) forms a partial and eroded hardground in which Middle Albian, *spathi* Subzone, phosphatized ammonite fragments are present as pebbles in pockets scoured out by the erosive submarine current activity.

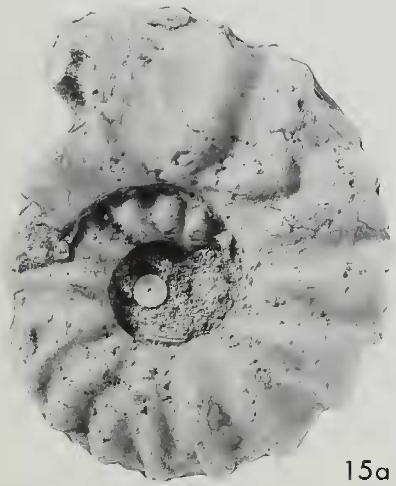
In north-west Kent and north Surrey, fossiliferous sediments of *puzosianus* Subzone age are separated from those of the '*eodentatus*' Subzone age by unfossiliferous sediments. In the Pays de Bray and Aube in northern France, however, this interval of time is represented by thick clays and loams with a rich fauna characterized by *Otohoplites bulliensis* Destombes.

The Carrière Ledoigt at St Martin l'hortier near Bully in the northern part of the Pays de Bray shows a sequence of shelly gault-like clays with a rich late-*mammillatum* Superzone fauna. The lower part of the sequence is characterized by *O. bulliensis* and is surmounted by a thin interval of clay containing *Otohoplites normanniae* Destombes, Juignet & Rioult (Destombes 1973, 1977*a*, *b*). The clays above this interval contain *Pseudosonneratia* (*Isohoplites*) *steinmanni* (Jacob). *Hoplites* (*Isohoplites*) *eodentatus* Casey (1961) is conspecific with *P.* (*I.*) *steinmanni* and the *eodentatus* Subzone of authors should in future be referred to as the *steinmanni* Subzone. In the late *mammillatum* Zone sequence exposed in the Carrière Ledoigt the first evidence of erosion and condensation occurs within the *steinmanni* Subzone clays.

The sequence in the northern Pays de Bray led Destombes (1973) to consider that it formed an uncondensed representation of the *raulinianus* Subzone of Casey, which he duly raised to the rank of a Zone. At that time, he recognized two Subzones within this Zone; an earlier Subzone of *O. bulliensis*, and a later Subzone of *O. normanniae* followed directly by the *eodentatus* Subzone without sedimentary break. On that occasion and in 1977, Destombes considered that sediments of *puzosianus* Subzone age preceded those classified with the *bulliensis* Subzone although there was no ammonite evidence to confirm his idea. Subsequently, Destombes (1979) recognized the Subzone of *Otohoplites larcheri* in the sequence exposed in the Bois de Perchois referred to above. Influenced incorrectly by his conclusion that the *bulliensis* Subzone sequence in the Pays de Bray was the equivalent of part of Casey's *raulinianus* Subzone, that the *larcheri* Subzone was also of *raulinianus* Subzone age in Casey's sense albeit earlier than the *bulliensis* Subzone, and that ammonite nuclei occurring in the clays between those of *floridum* Subzone age and those of *larcheri* Subzone age in the Bois de Perchois were those of *Protohoplites* (*Hemisonneratia*), Destombes concluded that the *puzosianus* Subzone preceded his *raulinianus* Zone. On this occasion, he divided his *raulinianus* Zone into an earlier, *larcheri*, Subzone and later, *bulliensis*, Subzone dropping altogether the *normanniae* Subzone having recognized that this species of *Otohoplites* ranges from the later part of the *bulliensis* Subzone into the *steinmanni* Subzone. The evidence of subzonal sequence in Kent, however, is unequivocal and the correct sequence of Subzones is *kitchini*, *floridum*, *raulinianus* (= *larcheri*), *puzosianus*, *bulliensis* (including *normanniae*) and *steinmanni* in ascending order. Just as in the case of south-east England where ammonites of *bulliensis* Subzone age have not yet been found in the

14a

14b



15a

15b

Figs 14, 15 *Otohoplites waltoni* Casey, both × 1.

Figs 14a, b Copy of Destombes' (1979, pl. 4–22, fig. 3 and pl. 4–18, fig. 4) illustrations of a paratype of *O. larcheri*, Bed 2b, Perchois Est quarry, Aube, Duffaud Coll. No. 4.

Figs 15a, b Holotype of *O. waltoni* Casey (1960–, pl. LXXXIII, figs 7a, b; note that fig. 7a is enlarged), Bed 33 phosphatic debris ex *raulinianus* Subzone, foreshore reefs, near Copt Point, Folkestone, Kent. BGS Zk 4844 R. Casey Coll.

unfossiliferous sediments between those of *puzosianus* age and those of *steinmanni* age, so also in France no sediments have yet been seen between those of definite '*larcheri*' age and those of *bulliensis* Subzone age. The full ammonite sequence can only be determined from a study of all available sections in England and in France.

Destombes recognized two Zones within the *mammillatum* Superzone. *Sonneratia dutempleana* (d'Orbigny) is employed as the index species for the earlier Zone and, as already noted, *Otohoplites raulinianus* is employed for the later Zone. Neither of these species is appropriate as a zonal index, although Destombes recognizes the important fact that in the European province the lower part of the *mammillatum* Superzone is characterized by species of *Sonneratia* and the later part by species of *Otohoplites*. However, his index ammonite for the earlier part of the Superzone, *Sonneratia dutempleana*, does not occur in that interval of time and is restricted to the *puzosianus* Subzone in the sense of Casey. It is unsuitable, therefore, as a zonal index.

Neither the typical *Otohoplites raulinianus* nor its common companion *Otohoplites waltoni* Casey (i.e. together the *O. larcheri* of Destombes) occur in the *bulliensis* and *steinmanni* Subzones deposits in the Carrière Ledoigt or in the Aube. Both species are confined to the *raulinianus* and *puzosianus* Subzones in Casey's sense. However, there are other species of *Otohoplites*, such as *O. auritiformis* (Spath), which have a range from the *raulinianus* Subzone into the *steinmanni* Subzone and which are, therefore, more appropriate candidates for selection as the zonal index in preference to the shorter-ranged *O. raulinianus*.

Amédro (1980)

Amédro (1980, 1981, 1984*a*, *b*) recognized a series of Assemblage Zones given below in Table 3. Fundamentally, Amédro and Destombes recognize the same ammonite faunal sequence, whether or not Amédro calls them Assemblage Zones and Destombes calls them Subzones. The *puzosianus* Subzone in this scheme, as in that of Destombes, is considered to follow directly upon the *floridum* Subzone and to precede the *larcheri* Subzone (the *raulinianus* Subzone of Casey). The evidence against this conclusion has been discussed in the preceding section of this paper. Additionally, Amédro introduces an Assemblage Zone of *Otohoplites auritiformis* between the *larcheri* and *bulliensis* Zones. Amédro did not provide a formal definition of his *auritiformis* Zone, nor a typical locality at which to assess its characteristic fauna. Presumably, it is based on the sequence developed in the Ardennes (e.g. Machéroménil) which contains the typical *O. raulinianus* (d'Orbigny) and *O. auritiformis* (Spath) (see Casey 1960–, 493, 509, 511). The principal phosphatic nodule bed from which these two ammonites come also contains *Sonneratia dutempleana* (d'Orbigny), *Protohoplites* (*Hemisonneratia*) spp. including *P.* (*H.*) *puzosianus* (d'Orbigny), *Protohoplites* (*Protohoplites*) spp. including *P.* (*P.*) *latisulcatus* (Sinzow), *Pseudosonneratia* (*Pseudosonneratia*) spp. including *P. typica* Spath, and *Tetrahoplites* spp. Although the phosphatic pebble bed at Machéroménil indicates condensation of a thickness of previously formed sediments, nonetheless the fauna mentioned above composes the indigenous element in Casey's Bed 33 at Folkestone (Bed 1a of Jukes-Browne) and of the the other

Table 3 Assemblage Zones recognized by Amédro (1980).

	Assemblage Zones
Middle Albian (part)	*Isohoplites eodentatus*
Equivalent of the *Douvilleiceras mammillatum* Zone	***Otohoplites normanniae***
	Otohoplites bulliensis
	Otohoplites auritiformis
	Otohoplites larcheri
	Protohoplites puzosianus
	Cleoniceras floridum
	Sonneratia kitchini
	Leymeriella regularis

puzosianus Subzone deposits elsewhere in Kent and northern Surrey. Amédro's Assemblage Zone of *O. auritiformis* represents the same time interval as Casey's Subzone of *P.* (*H.*) *puzosianus*.

Amédro continues to use Destombes' Subzone of *Otohoplites normanniae*, referring to it as an Assemblage Zone. As mentioned earlier, *O. normanniae* Destombes, Juignet & Rioult is not only characteristic in the later-deposited sediments of the *bulliensis* Subzone, but occurs also in the *steinmanni* Subzone (e.g. Destombes 1973, 1977*a*) where it is not uncommon. Its use as an index of an Assemblage Zone intervening between that of *O. bulliensis* and *P.* (*I.*) *steinmanni* is, therefore, misleading.

Savel'ev (1973, 1974)

The best-documented biostratigraphical account of the *mammillatum* Superzone sequence (the Zone of *Cleoniceras mangyschlakense*) in the European region of the Soviet Union is that given by Savel'ev (1973*a*, *b*, 1974) for the sequence exposed in the Mangyschlak Peninsula, Transcaspia. His zonal and subzonal scheme (1973*b*, 1974) is given here in Table 4. The zonal index species *C. mangyschlakense* Luppov is a subjective junior synonym of *Cleoniceras* (*Neosaynella*) *platydorsatum* (Sinzow) as indicated by Casey (1960–, 574).

At first glance, this scheme appears to be radically different from that recognized by Casey (1961) in western Europe. Although a full monographic treatment of the superb *mammillatum* Superzone ammonite fauna collected *in situ* in the Mangyschlak sequence has still to be published, the ammonites listed and figured so far, especially by Savel'ev (e.g. 1973*a*, *b*, 1974, 1981), indicate that the differences are more apparent than real. He, like Destombes, recognizes an earlier interval characterized by *Sonneratia* and a later interval characterized by *Otohoplites*.

The *Sonneratia kitchini* Subzone of Casey is represented in the Mangyschlak Peninsula sequence by relatively thick sediments which Savel'ev (1973*b*, 1974) classified with an earlier Subzone of *Sonneratia* (*Globosonneratia*) *globulosa* Savel'ev and a later Subzone of *Sonneratia* '(*Eosonneratia*)' *solida* Savel'ev. Both Subzones contain species of *Sonneratia* closely comparable to those of the highly condensed English *kitchini* Subzone deposits. Indeed, *S.* (*G.*) *globulosa* Savel'ev (1973*b*, 84; pl. 24, figs 1a–c) is the inner whorls of *Sonneratia perinflata* Breistroffer, a comparison being given here in Figs 16 and 17.

The overlying Subzone of *Sonneratia* '(*Eosonneratia*)' *rotula* Savel'ev may belong to the western European *Cleoniceras floridum* Subzone as does the following Subzone of *Sonneratia* '(*Eosonneratia*)' *strigosa* Savel'ev. *S.* '(*E.*)' *rotula* Savel'ev (1973*b*, 82; pl. 23, figs 3a–c) is closely comparable to the holotype of *Sonneratia ciryi compressa* Destombes (1979, 81; pl. 4–10, figs 3a, b) from Bed 1b of the Perchois Ouest quarry (*floridum* Subzone), Aube, France. The original figures of these two ammonites are reproduced here in Figs 20 and 21. *S.* '(*E.*)' *strigosa* Savel'ev (1973*b*, 82; pl. 23, figs 4a, b) is also present in Bed 1b of the Perchois Ouest quarry described

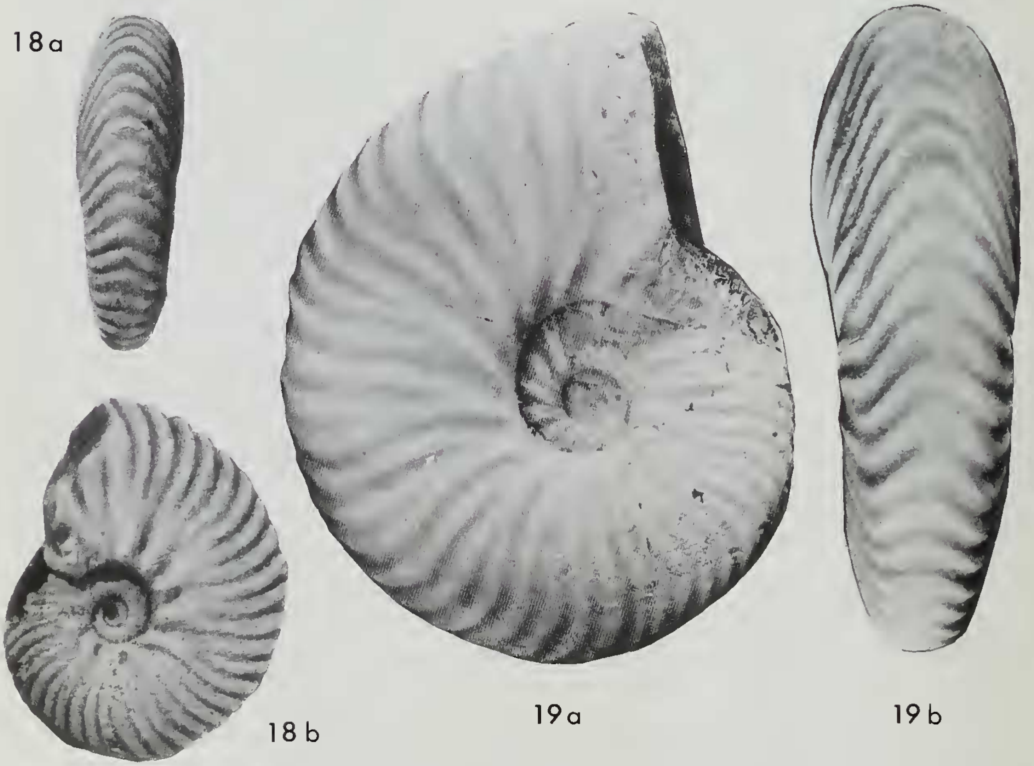
Table 4 Zonal and subzonal scheme recognized by Savel'ev (1973*b*, 1974) in the Mangyschlak Peninsula, Transcaspia, USSR.

Superzone	Zone	Subzone
[Middle Albian] part	*Hoplites dentatus* (part)	*Pseudosonneratia* (*Isohoplites*) *eodentata*
Cleoniceras mangyschlakense	*Otohoplites sinzowi*	*Otohoplites crassus* *Tetrahoplites suborientalis*
	Sonneratia vnigri	*Sonneratia strigosa* *Sonneratia rotula* *Sonneratia solida* *Sonneratia globulosa*
	Leymeriella (*Neoleymeriella*) *regularis*	

Figs 16, 17 *Sonneratia* (*Globosonneratia*) *perinflata* Breistroffer, both × 1.

Figs 16a–c Copy of Savel'ev (1973*b*, pl. 24, figs 1a–c), holotype of *S.* (*Globosonneratia*) *globulosa* Savel'ev, *globulosa* Subzone, Mangyschlak, for comparison with:

Figs 17a, b Inner whorls of a typical example of *Sonneratia perinflata* Breistroffer, Nodule Band II, Gault–Lower Greensand Junction Beds, Arnold's pit, Billington Crossing, Leighton Buzzard, Bedfordshire. BMNH C90539, C. W. & E. V. Wright Coll. See also Figs 33a, b.



Figs 18, 19 *Sonneratia caperata* Casey, both × 1.

Figs 18a, b Copy of Savel'ev (1973*b*, pl. 23, figs 4a, b), holotype of *Sonneratia* (*Eosonneratia*) *strigosa* Savel'ev, *strigosa* Subzone, Mangyschlak.

Figs 19a, b Specimen figured by Destombes (1979, pl. 4–11, figs 1a, b) as *S. daguini* Destombes transitional to *S. tenuis* Sinzow, Bed 1b (*floridum* Subzone), Perchois Ouest quarry, Aube, Destombes Coll. No. 224.

under the name of *Sonneratia daguini* Destombes (1979, 83; pl. 4–11, figs 1–3). The original figures of these two ammonites are reproduced here in Figs 18 and 19. A closely comparable, if not conspecific, form was described as *Sonneratia caperata* by Casey (1965, 537; pl. LXXXVII, figs 2a, b) which is also of *floridum* Subzone age (Casey 1980, 660).

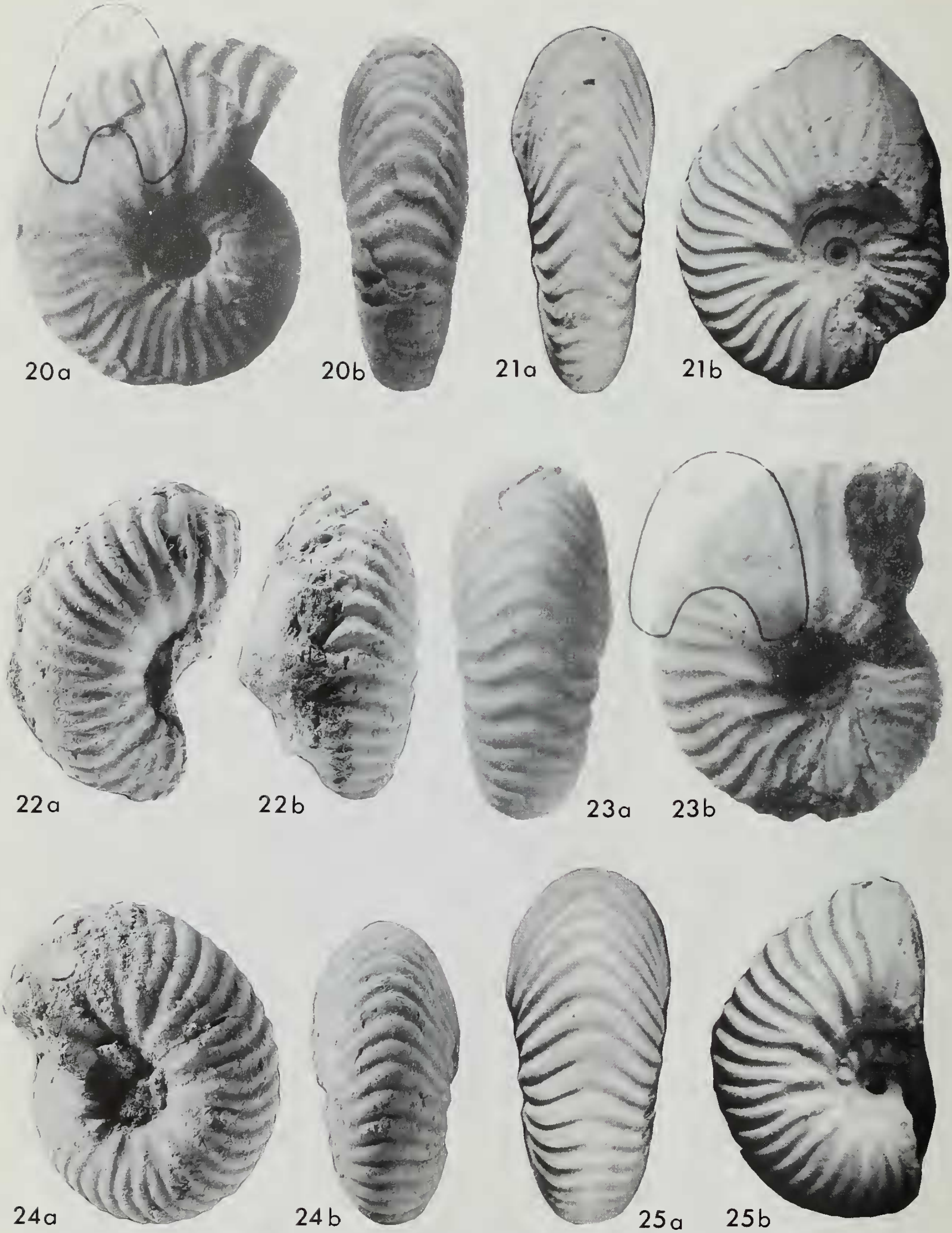
It is significant that the holotype of Savel'ev's zonal index fossil, *Sonneratia* '(*Eosonneratia*)' *vnigri* Savel'ev (1973*b*, 80; pl. 23, figs 2a–c) is almost identifical with the holotype of *Sonneratia ciryi ciryi* Destombes (1979, 83; pl. 4–10, figs 2a, b) found in Bed 1b of the Perchois Ouest quarry. The original figures are reproduced here in Figs 23 and 25. In view of the Russian sequence with its wealth of *Sonneratia*, and of the English *floridum* Subzone sequence in which *Sonneratia* is rare, it is possible that the cementstone concretions of Bed 1b of the Perchois Ouest quarry, which contain both *S.* '(*E.*)' *strigosa* and *S.* '(*E.*)' *rotula*, might be a cumulate produced by very gentle current winnow. *S.* (*S.*) *vnigri* is known from the condensed *floridum* and *raulinianus* Subzones debris in Casey's Bed 33 at Folkestone (Casey 1960–, pl. LXXXVII, figs 5a, b and herein in Fig. 24).

There is no ammonite evidence for the presence of the *raulinianus* (*larcheri*) fauna in Mangyschlak. The *floridum* (*strigosa*) Subzone sediments are overlain by deposits classified by Savel'ev with a Subzone of *Tetrahoplites suborientalis*. This Subzone contains species of *Protohoplites* (*Protohoplites*) and *Protohoplites* (*Hemisonneratia*) as well as species of *Tetrahoplites*, characteristic elements of the western European *puzosianus* Subzone. Superficially, it would appear that the Mangyschlak sequence supports the view of Destombes and Amédro that the *puzosianus* Subzone follows directly upon the *floridum* Subzone. However, at the junction of the sediments of *strigosa* and *suborientalis* age there is evidence of erosion with cobble concretions (e.g. Savel'ev 1973*a*, 20).

Further evidence of the true faunal sequence in the *mammillatum* Superzone is provided by the ammonites of Savel'ev's Subzone of *Otohoplites crassus* which follows upon that of *Tetrahoplites suborientalis*. The fauna is closely comparable to that of Destombes' Subzone of *O. bulliensis* and there is no evidence of an intervening '*larcheri*' Subzone fauna in the Mangyschlak sequence. Strictly speaking, however, the absence of the sediments of *raulinianus* (*larcheri*) Subzone age in Mangyschlak precludes a solution of the problem of subzonal superposition in this section. Equally, it does not negate the evidence of faunal succession determined in south-east England.

The *bulliensis* Subzone is well represented in the Mangyschlak sequence where this time interval is indexed by *Otohoplites crassus* Savel'ev. The papers describing stratigraphically significant species of *Otohoplites* from this Subzone in France and the Soviet Union appeared within a few weeks of each other (Destombes 19th November 1973; Savel'ev 1973*b* in December). *Otohoplites bulliensis* Destombes (1973, pl. 1, figs 1, 1a) is not the subject of any nomenclatorial problem and, as his paper has date priority, it is employed here as the subzonal index instead of *Otohoplites crassus* Savel'ev. The specimen of '*Otohoplites* aff. *raulinianus* (d'Orb.) transit ad *O. destombosi* Casey' (*sic*) from the Carrière Ledoigt, St Martin l'hortier, Pays de Bray, France, figured by Destombes (1973, pl. 1, figs 5, 5a) is conspecific with the holotype of *O. crassus* Savel'ev (1973*b*, 86–7; pl. 24, figs 3a–c). The specimen of *Otohoplites* aff. *subhilli* (Spath) figured by Destombes (1973, pl. 1, figs 3, 3a) is conspecific with the holotype of *Otohoplites venustus* Savel'ev (1973*b*, 87; pl. 25, figs 1a–c), which is itself almost identical to the holotype of *O. subhilli* (Spath) figured by Sinzow (1909, pl. II, figs 19, 20). All five original figures are re-figured here in Figs 26–30. A closely comparable fauna exists, therefore, at these two widely separated localities in France and the Soviet Union at the western and eastern margins of the European province.

Savel'ev includes the *puzosianus* Subzone (his *suborientalis* Subzone) and the *bulliensis* Subzone (his *crassus* Subzone) in a Zone of *Otohoplites sinzowi*. The holotype of *O. sinzowi* Savel'ev (1973*b*, 85–6; pl. 24, figs 4a–c) re-figured here in Fig. 38 is very close to *Otohoplites auritiformis* (Spath) and is considered here to fall within the range of morphological variation of a single species of *Otohoplites* for which Spath's name has priority. *Otohoplites glyphus* Casey (1960–, 509, text-fig. 191a, b), the holotype of which is from the same bed and locality (Machéroménil) as the neotype of *O. auritiformis*, might also prove to be a subjective synonym



Figs 20–25 Comparisons of Russian and western European species of *Sonneratia* (*Sonneratia*), all × 1.

Figs 20a, b Holotype of *Sonneratia* (*Eosonneratia*) *rotula*. Copy of Savel'ev (1973*b*, pl. 23, figs 3a, b) from the *rotula* Subzone, Mangyschlak, for comparison with:

of that latter species. The neotype possesses a malformed body chamber (Casey 1960–, 509, text-fig. 191c–e) which, superficially, makes *O. auritiformis* appear to be different. Yet another example, identified by Casey (1960–, pl. LXXXV, fig. 1) as *O. glyphus*, forms part of the indigenous fauna of his Bed 33 (Bed 1a) at Folkestone (and therefore of *puzosianus* Subzone age) and is re-figured here in Fig. 36. Savel'ev's choice of this morphotype as a zonal index is well-founded. *O. auritiformis*, as interpreted here, has a pre-mutation in the *raulinianus* Subzone (e.g. the specimen figured here in Fig. 37), the typical form of the *puzosianus* Subzone and a late form in the *bulliensis* Subzone. A rare related form occurs in the *steinmanni* Subzone.

The Subzone of '*Hoplites* (*Isohoplites*) *eodentatus*'

Since the description of *Hoplites* (*Isohoplites*) by Casey (1954), and of the species *H.* (*I.*) *eodentatus* by Casey (1961), the relative period of time in which they occur had been included in the Middle Albian (basal *Hoplites dentatus* Zone). As such, a detailed description of sediments representing this Subzone in England and France was published in the author's work on the Middle Albian deposits in the Anglo-Paris Basin (Owen 1971). More recent work has made it necessary to revise the nomenclature of this time interval and to transfer it to the Lower Albian as the terminal Subzone of the *mammillatum* Superzone (Owen 1984, 1985).

The type species of *Isohoplites* is *Parahoplites steinmanni* Jacob. A comparison of the holotype of Casey's species *H.* (*I.*) *eodentatus* (Casey 1961, pl. 83, figs 4a, b; GSM 98602 now lost) with the lectotype and paralectotype of *Isohoplites steinmanni* (Jacob) figured by Casey (1960–, 538, text-figs 202a–f) shows that they are conspecific, a conclusion arrived at more recently by Amédro 1984*b*). Casey (1954) considered that *Isohoplites* on balance should be included in *Hoplites* rather than in *Pseudosonneratia* because of the tendency of the ribs to become effaced along the siphonal line as they swing across the venter. Neither Savel'ev (e.g. 1976) nor the writer consider this feature to be of sufficient burden to separate *Isohoplites* from the group of more discoidal species of *Pseudosonneratia* which occur from the *puzosianus* Subzone onward. The systematic position of *Isohoplites* is discussed in a later section of this paper dealing with the genus *Pseudosonneratia.* It is necessary here to alter the nomenclature of the Subzone to that of *Pseudosonneratia* (*Isohoplites*) *steinmanni* which will be used throughout the remainder of this paper.

The ammonite fauna of the *steinmanni* Subzone (e.g. Owen 1971), although foreshadowing that of the early Middle Albian, has a distinct *mammillatum* Superzone aspect. *Otohoplites* is still present together with rare *Cleoniceras* as well as the species of *Pseudosonneratia* (*Isohoplites*). *Douvilleiceras* and *Beudanticeras* are common, although both genera continue on into the Middle Albian. The lyelliceratid ammonite *Tegoceras*, which occurs from the *floridum* Subzone onward, is well represented in the *steinmanni* Subzone in the regions of the European shelf seas opening into the Tethys. At the end of the Subzone, *Tegoceras* passes rapidly through a '*pseudolyelli*' stage to produce species of *Lyelliceras* such as *L. lyelli* (Leymerie). Like its *Tegoceras* ancestors, *L. lyelli* is of widespread interprovincial occurrence and is an ideal marker for the recognition of the base of the Middle Albian Substage. A formal recommendation to

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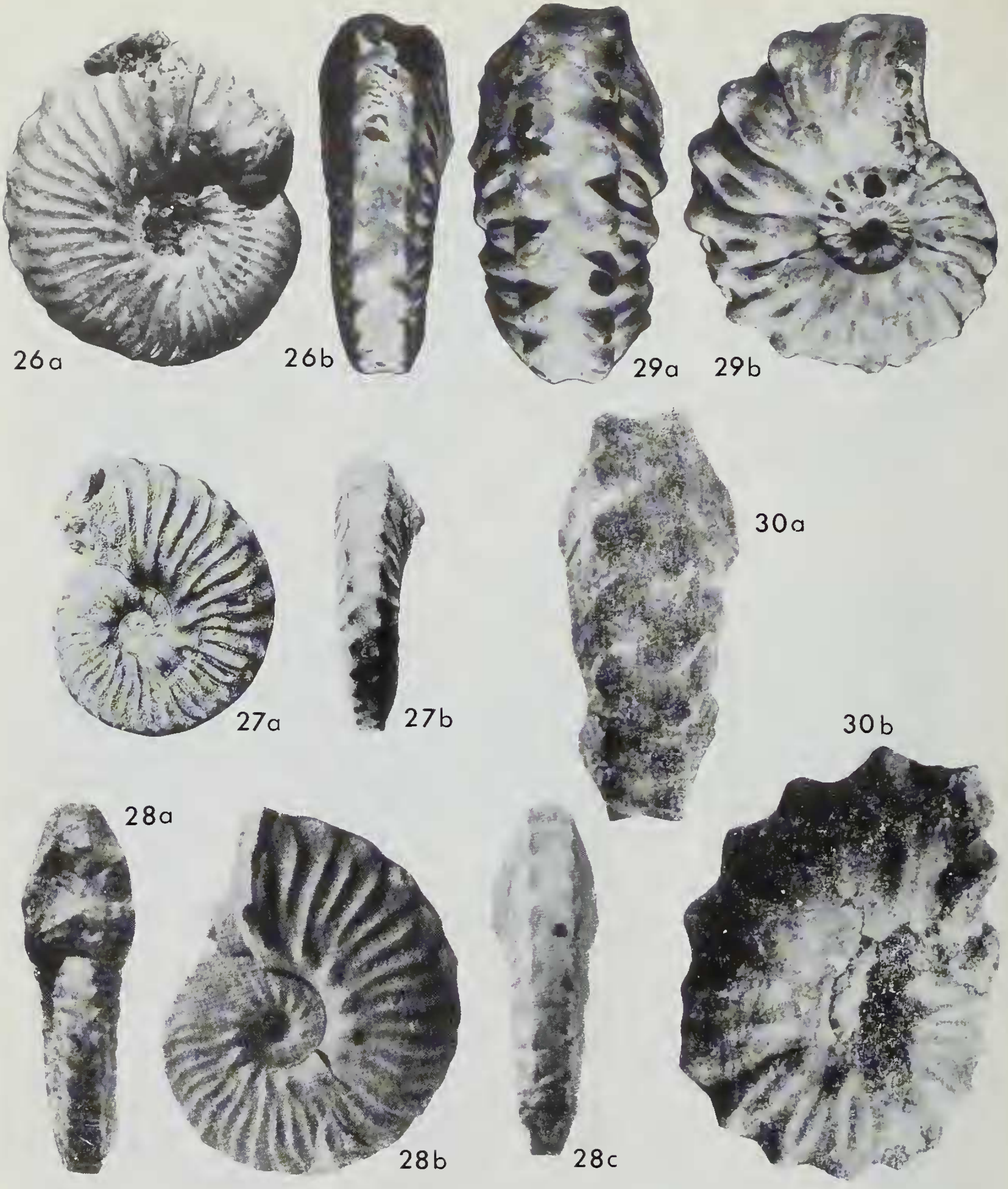
Figs 21a, b *Sonneratia ciryi compressa* Destombes. Copy of Destombes (1979, pl. 4–10, figs 3a, b), Bed 1b (*floridum* Subzone), Perchois Ouest quarry, Aube, Destombes Coll. No. 235.

Figs 22a, b *Sonneratia* (*Sonneratia*) *dutempleana* (d'Orbigny), *puzosianus* Subzone, Ford Place pit, near Trottiscliffe, Kent. BMNH C84748 C. W. & E. V. Wright Coll. No. 18528 (figured Casey 1960–, pl. LXXXVIII, figs 2a, b), for comparison at subgeneric level with:

Figs 23a, b *Sonneratia* (*Sonneratia*) *vnigri* Savel'ev (type species of the subgenus *Eosonneratia* Savel'ev, figured 1973*b*, pl. 23, figs 2a, b), *sinzowi* Zone, Mangyschlak.

Figs 24a, b *Sonneratia* (*Sonneratia*) *vnigri* Savel'ev. Specimen figured by Casey (1960–, pl. LXXXVII, figs 5a, b) as *Sonneratia* cf. *parenti* Jacob, Bed 33 (phosphatic debris of mixed *floridum* and *raulinianus* Subzones age), East Wear Bay, Folkestone, Kent. R. Casey Coll. BGS GSM 70405.

Figs 25a, b *Sonneratia* (*Sonneratia*) *vnigri* Savel'ev. Copy of the original illustrations of the holotype of *Sonneratia ciryi ciryi* Destombes (1979, pl. 4–10, figs 2a, b), Bed 1b (*floridum* Subzone), Perchois Ouest quarry, Aube, Destombes Coll. No. 101.



Figs 26–30 Comparison of Russian and western European *bulliensis* Subzone species of *Otohoplites*. All × 1.

Figs 26a, b *Otohoplites* aff. *subhilli* (Spath), robust dimorph. Copy of Destombes (1973, pl. 1, figs 3, 3a), Bed 4a (*bulliensis* Subzone), Carrière Ledoigt, St Martin l'hortier, Pays de Bray.

Figs 27a, b Holotype of *Otohoplites subhilli* (Spath). Copy of the original figures of Sinzow (1909, pl. Il, figs 19, 20), Mangyschlak.

Figs 28a, b *Otohoplites subhilli* (Spath). Holotype of *Otohoplites venustus* Savel'ev; copy of the original figures of Savel'ev (1973*b*, pl. 25, figs 1a–c), *crassus* Subzone, Mangyschlak.

Figs 29a, b *Otohoplites crassus* Savel'ev. Copy of the specimen figured by Destombes (1973, pl. 1, figs 5, 5a) identified as '*Otohoplites* aff. *raulinianus* (d'Orb.) transit ad O. *destombosi* Casey' (sic), Bed 4a (*bulliensis* Subzone), Carrière Ledoigt, St Martin l'hortier, Pays de Bray.

Figs 30a, b *Otohoplites crassus* Savel'ev. Copy of the figures of the holotype (Savel'ev 1973*b*, pl. 24, figs 3a, b), *crassus* Subzone, Mangyschlak.

that effect was made in Copenhagen in 1983 (Owen 1984, 1985). The *steinmanni* Subzone is, therefore, the latest recognized Subzone of the *mammillatum* Superzone of the Lower Albian Substage.

Proposed new zonal and subzonal scheme

The scheme of Zones and Subzones grouped together in a Superzone of *Douvilleiceras mammillatum*, proposed here, is set out in Table 5 and is defined below.

Table 5 Zonal and subzonal scheme of the *D. mammillatum* Superzone proposed here for the European faunal province.

Superzone	Zone	Subzone
Douvilleiceras mammillatum	*Otohoplites auritiformis*	*Pseudosonneratia (Isohoplites) steinmanni*
		Otohoplites bulliensis
		Protohoplites (Hemisonneratia) puzosianus
		Otohoplites raulinianus
	Sonneratia chalensis	*Cleoniceras floridum*
		Sonneratia kitchini
		Sonneratia (Globosonneratia) perinflata

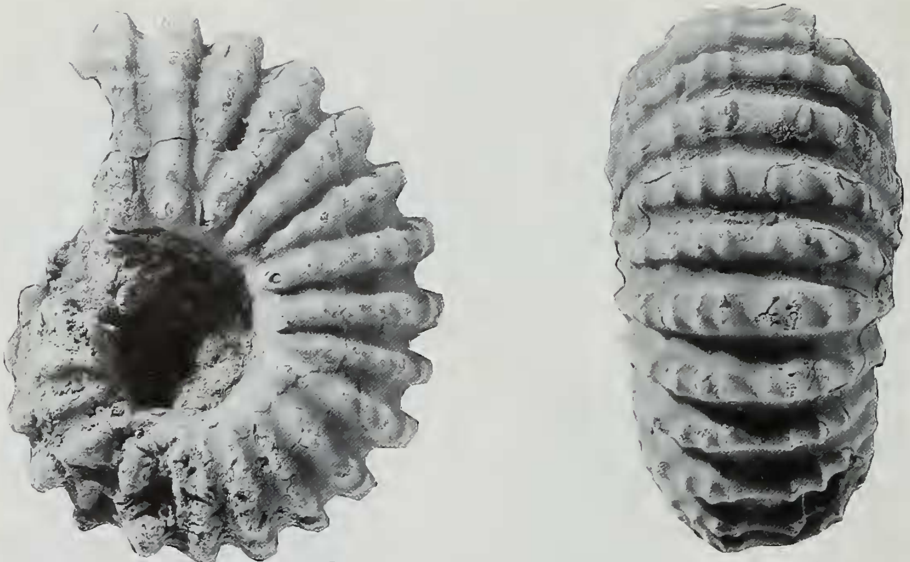
The Superzone of *Douvilleiceras mammillatum* (Destombes 1979 emended herein)

Figs 31a, b

The genus *Douvilleiceras* is almost cosmopolitan in its distribution throughout its total time range. Stemming from a cheloniceratid root stock in the Aptian via *Eodouvilleiceras*, the first known occurrence of *Douvilleiceras* is in the *regularis* Subzone of the *Leymeriella tardefurcata* Zone where it is relatively uncommon (Casey 1960–, 263). The acme of its development is reached within the *mammillatum* Superzone, but it extends onward into the early Middle Albian *Lyelliceras lyelli* Subzone where it is occasionally common. It does not survive the end of the *lyelli* Subzone. There are a number of records of the association of *Douvilleiceras* and *Lyelliceras* outside the European province which are dated as Lower Albian because of the presence of *Douvilleiceras*. These associations are in fact of early Middle Albian, *Lyelliceras lyelli* Subzone, age.

Douvilleiceras mammillatum (Schlotheim) is a species subject to a marked degree of individual morphological variation. Interpreted in this sense, its time range extends from the *Sonneratia* (*Globosonneratia*) *perinflata* Subzone (*D. mammillatum aequinodum* (Quenstedt)) up to the *steinmanni* Subzone. The Superzone of *Douvilleiceras mammillatum* can be regarded, therefore, as a total range Superzone. While providing at Superzone level an index of relative time of almost cosmopolitan extent, a single 'Zone' of *D. mammillatum* is not suitable for the European province. The scattered and incomplete nature of sediments representing the *mammillatum* Superzone in Europe makes it desirable to reflect in the scheme of Zones the distinction between an early period characterized by *Sonneratia* ('*Eosonneratia*') and a later period characterized by *Otohoplites*, in a similar manner to that attempted by Savel'ev (1973*b*, 1974) and Destombes (1979). It might not be possible to identify positively a specific Subzone in an incomplete or sparsely fossiliferous sequence, but if a bed yields a species of *Sonneratia* of the *chalensis–flava* group on the one hand, or a species of *Otohoplites* on the other, it is possible to determine whether the bed is of early or late *mammillatum* Superzone age respectively.

The Superzone of *Cleoniceras mangyschlakensis*, recognized by Savel'ev (1973*b*, 1974) in the Soviet Union, reflects the relative paucity of the occurrence of *Douvilleiceras* in the eastern regions of the European province at a distance from the seaways linking with the Tethyan province. *C. mangyschlakensis* Luppov is conspecific with *Cleoniceras* (*Neosaynella*) *platydorsatum* (Sinzow), a species which does not range throughout the *mammillatum* Superzone.



31a 31b

Figs 31a, b *Douvilleiceras mammillatum* (Schlotheim). The Superzone index species. Neotype, BMNH C12491 F.G.H. Price Coll. × 1. By preservation from Bed 33 (Casey 1961), condensed *floridum* and *raulinianus* Subzones debris, near Copt Point, Folkestone, Kent.

Although it is recommended here that the *mangyschlakensis* Superzone be abandoned, this should not prove a difficulty to Soviet workers because the two Zones defined below can be recognized as easily in the Soviet Union as they can in western Europe. The stratigraphical distribution of the ammonite fauna known at present is given in Table 6, and the index ammonites are figured in Figs 31–42.

The Zone of *Sonneratia chalensis* (new Zone)

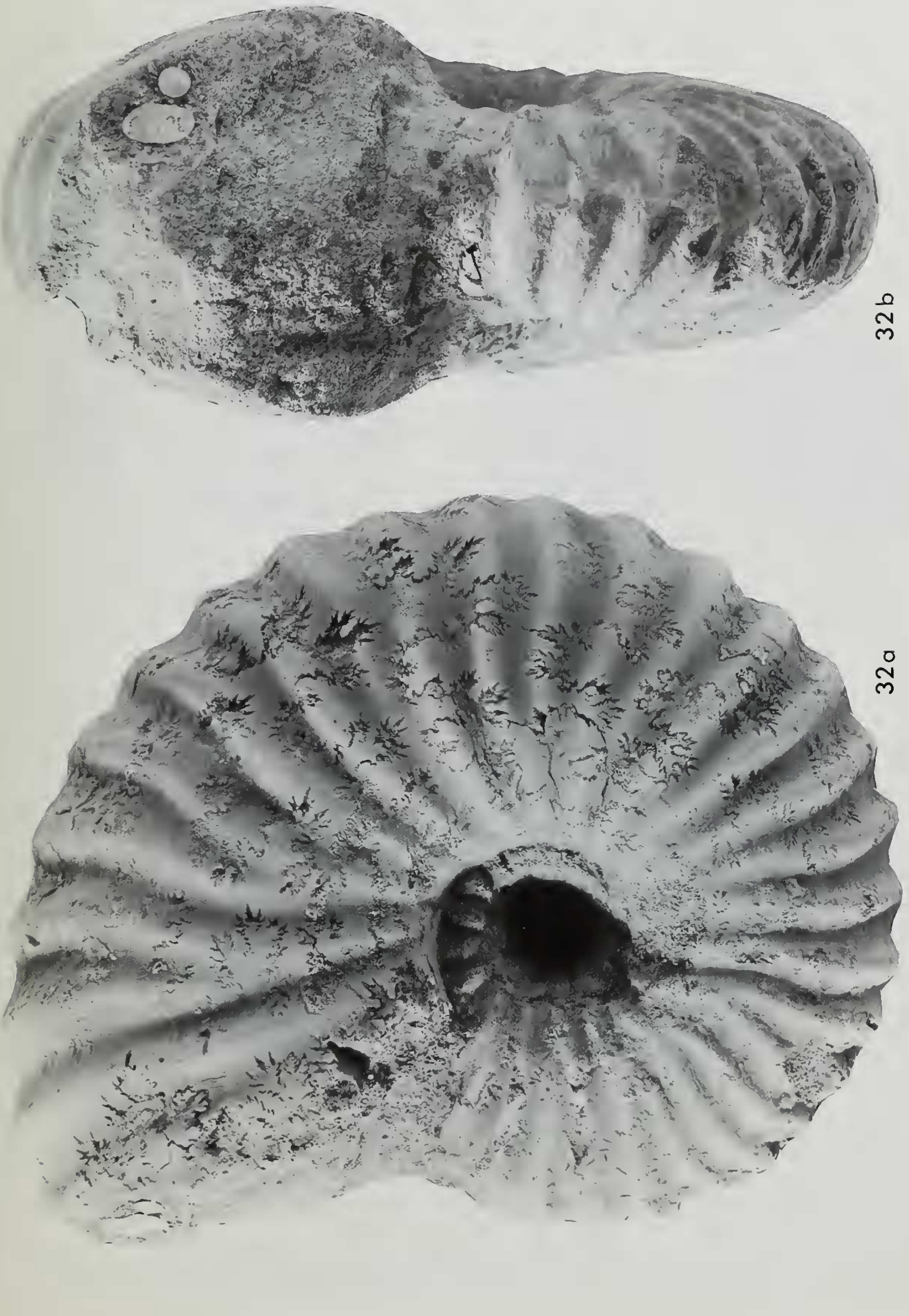
Figs 32a, b

The early part of the *mammillatum* Superzone is well developed in the Mangyschlak Peninsula, Transcaspia, USSR (e.g. Savel'ev 1973*a*, *b*, 1974). Unfortunately, the ammonite fauna as a whole has still to be fully monographed and it is not possible at this time to recognize a species in the Soviet Union which has a total range from the base of the *Sonneratia* (*Globosonneratia*) *perinflata* Subzone to the end of the *Cleoniceras floridum* Subzone.

The zonal index ammonite *Sonneratia* '(*Eosonneratia*)' *vnigri*, proposed by Savel'ev to encompass this period of time, is known to occur in western Europe only in deposits of *floridum* Subzone age and is, therefore, unsuitable for use in that role. On the other hand, *Sonneratia* (*Sonneratia*) *chalensis* Casey has a premutation in the *perinflata* Subzone, occurs typically in the *kitchini* Subzone and is replaced in the *floridum* Subzone by the closely related *Sonneratia* (*S.*) *flava* Casey.

Subzone of *Sonneratia* (*Globosonneratia*) *perinflata* (Savel'ev 1973*b* emended)
Figs 33a, b

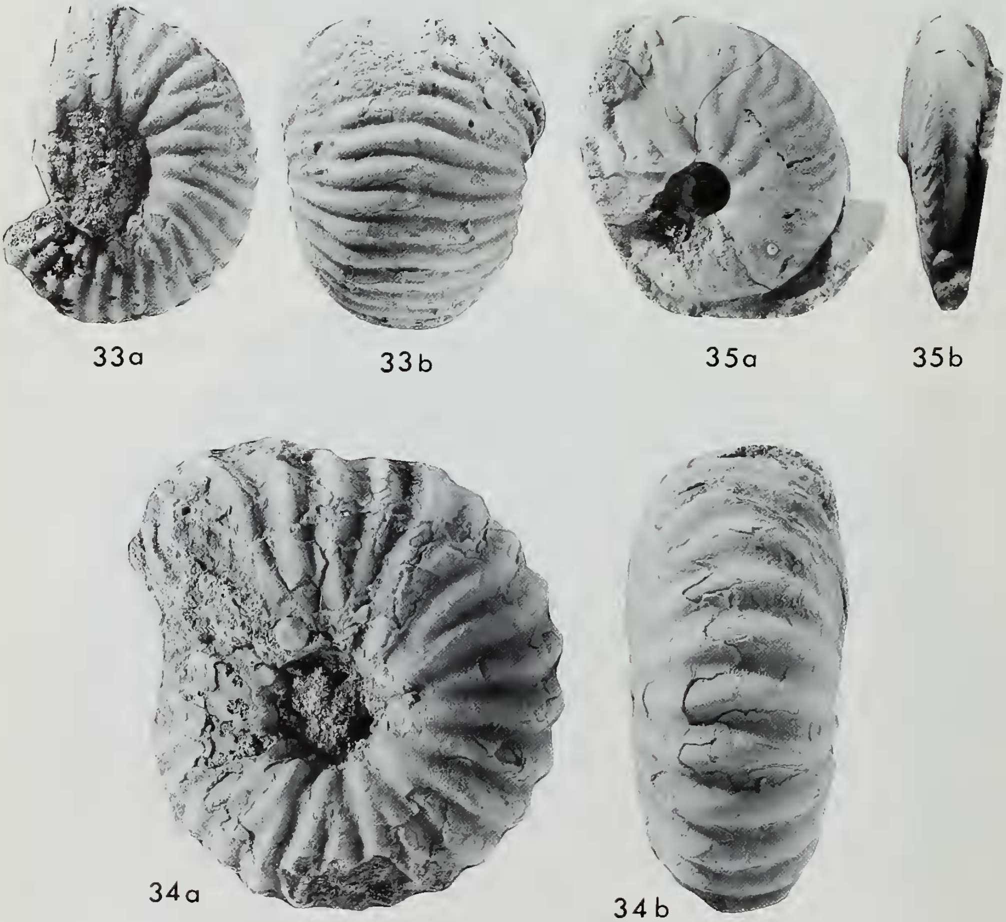
Savel'ev (1973*b*) recognized two Subzones corresponding to the English *kitchini* Subzone of Casey (Owen 1985). The earlier of these was indexed by Savel'ev with a juvenile ammonite described under the name *Sonneratia* (*Globosonneratia*) *globulosa*. This ammonite falls well within the morphological range of *Sonneratia* (*Globosonneratia*) *perinflata* Breistroffer (Figs 16, 17). In England, the typical *Sonneratia* (*Sonneratia*) *kitchini* Spath and *S.* (*G.*) *perinflata* occur



Figs 32a, b *Sonneratia (Sonneratia) chalensis* Casey. The earlier *mammillatum* Superzone zonal index species. BGS GSM 30695 Mrs R. Barrow Coll. × 1, coprolite workings opposite the Chequers Public House, West Dereham, Norfolk.

together only in the condensed *regularis* to *floridum* Subzones nodule beds in the Leighton Buzzard district, Bedfordshire. At West Dereham (Norfolk), however, the ammonite fauna is more restricted and *S.* (*G.*) *perinflata* is associated with *S.* (*S.*) *chalensis*, but not the typical *S.* (*S.*) *kitchini*. In the lower part of the Carstone Member of the Lower Greensand in the Isle of Wight, the typical *S.* (*S.*) *chalensis* is associated with *S.* (*S.*) *kitchini* but *S.* (*G.*) *perinflata* has not been found.

Sediments of *Sonneratia chalensis* Zone age are very sparse and scattered in occurrence in England. However, in view of the well developed sequence in the Mangyschlak Peninsula it is possible to detect two separate faunas in sediments formerly classified with the *kitchini* Subzone from the associations referred to above. The *S.* (*G.*) *perinflata* Subzone appears to be represented at West Dereham without the admixture of earlier, *regularis* Subzone, or later, *kitchini*



Figs 33–35 *Sonneratia chalensis* Zone subzonal indices. All × 1.

Figs 33a, b *Sonneratia* (*Globosonneratia*) *perinflata* Breistroffer. Holotype BMNH C40129 G. W. Coles Coll. Band III Gault–Lower Greensand Junction Beds, Arnold's Billington Crossing pit, Leighton Buzzard, Bedfordshire.

Figs 34a, b *Sonneratia* (*Sonneratia*) *kitchini* Spath BMNH C40346, same collection, horizon and locality as Fig. 33.

Figs 35a, b *Cleoniceras* (*Cleoniceras*) *floridum* Casey BMNH C72232 Author's Coll. Bed 7 (Casey 1961), Gault–Lower Greensand Junction Beds, Squerryes Estate Sand pit, Covers Farm, Westerham, Kent.

Subzone, ammonite faunas. In the Leighton Buzzard area, however, polyphase erosion has produced phosphatic nodule beds in which ammonites of the *regularis* Subzone (*tardefurcata* Zone), *perinflata* and *kitchini* Subzones are mixed together (e.g. Owen 1972). There is no other known occurrence of *perinflata* Subzone sediments in England. In France, the Subzone might be represented in the Perte du Rhône sequence (e.g. Casey 1960–, 527).

Subzone of *Sonneratia* (*Sonneratia*) *kitchini* (Casey 1961 emended herein)
Figs 34a, b

As now restricted, the *kitchini* Subzone corresponds to the Subzone of *Sonneratia* '(*Eosonneratia*)' *solida* of Savel'ev (1973*b*). The holotype of *S.* (*S.*) *solida* Savel'ev is a body chamber fragment of a coarsely ribbed form closely related to *Sonneratia* (*S.*) *rotator* Casey from the basal part of the Carstone Member of the Lower Greensand in the Isle of Wight. *S.* (*S.*) *rotator* and *S.* (*S.*) *kitchini* occur together both in the basal Carstone in the Isle of Wight and in Bed 3 of Casey (1961) at the base of the Gault–Lower Greensand Junction Beds in the Squerryes Estate sandpit, near Westerham, Kent. It is significant also that Savel'ev (1974, 118) records the occurrence of *S.* (*E.*) cf. *kitchini* in his *solida* Subzone fauna in Mangyschlak. Apart from the basal part of the Carstone Member in the Isle of Wight and Bed 3 at Westerham, the other localities in England in which *kitchini* Subzone sediments are known without admixture of earlier or later material are Bed 28 (Casey 1961) at East Cliff, Folkestone, and Eastwell Lane near Ashford, Kent. Elsewhere in England, in East Sussex (Casey 1961) and in the Leighton Buzzard district, Bedfordshire, *kitchini* Subzone ammonites are mixed with earlier, *regularis* Subzone ammonites, and debris derived from various *chalensis* Zone horizons.

In France, the ammonites of this Subzone such as *S.* (*S.*) *kitchini* and *S.* (*S.*) *rotator* have been found in the mixed late *tardefurcata* and early *mammillatum* Superzone phosphatic debris in the region of Machéroménil, Ardennes, and a form close to *S.* (*S.*) *rotator* has been recorded from the Perte du Rhône, Ain (Casey 1960–, 522, 526). The possibility of a *kitchini* Subzone age for the clays underlying the *floridum* Subzone sequence in the Bois de Perchois (Destombes 1979) is not yet supported by ammonite evidence.

Subzone of *Cleoniceras* (*Cleoniceras*) *floridum* (Casey 1961)
Figs 35a, b

The *floridum* Subzone is well represented in the Soviet Union, France and England. Savel'ev (1973*b*, 1974) has recognized two distinct Subzones within the Mangyschlak sequence corresponding to the *floridum* Subzone of western Europe; an earlier Subzone of *Sonneratia* '(*Eosonneratia*)' *rotula* and a later Subzone of *Sonneratia* '(*Eosonneratia*)' *strigosa*. However, in western Europe, both of Savel'ev's subzonal indices are known to be associated with *Cleoniceras* (*C.*) *floridum* Casey. It is perhaps significant that *S.* (*S.*) *rotula* Savel'ev and *S.* (*S.*) *strigosa* Savel'ev occur together in the little condensed sequence in Bed 1b of the Bois de Perchois, Aube (see supra p. 184), with its magnificent *floridum* Subzone fauna. It is possible that the cement stone nodules of Bed 1b represent a gentle accumulation of debris from several horizons within the *floridum* Subzone by gentle current winnow, but there is no certain evidence of such activity in the sedimentology of this bed. In England, the occurrence of *Sonneratia* and early *Pseudosonneratia* in deposits of *floridum* Subzone age is rare. *S.* (*S.*) *caperata* Casey, which is probably conspecific with *S.* (*S.*) *strigosa* (in which case Casey's name would have priority of usage), occurs in *floridum* Subzone sediments in Kent (e.g. Casey 1960–, 660). It seems unlikely that this difference in the abundance of *Sonneratia* and *Pseudosonneratia* is due to small scale provincialism, and in view of the Mangyschlak sequence, there is a strong possibility that the *floridum* Subzone sediments of southern England are slightly later than those of Bed 1b of the Bois de Perchois, Aube. As in the case of the sediments classified with the *kitchini* Subzone in the sense of Casey (1961), it is possible that the two Subzones recognized in the Mangyschlak sequence corresponding to the *floridum* Subzone of western Europe may be recognizable in the scattered and incomplete sequences seen in France and England.

The *floridum* Subzone sequence in England has been described by Casey (1961) in some detail with additions by Owen (1972). Little condensed, but thin, sediments of this age are known in the more basinal areas of deposition in north-west Kent and east Surrey, capped by a phosphatic pebble bed containing a fauna belonging solely to this Subzone. Elsewhere in Kent and Surrey, *floridum* Subzone sediments have been altogether removed by current scour or, as in the case of Bed 33 at Folkestone, the phosphatic debris has been mixed subsequently with that derived from *raulinianus* Subzone sediments during a later period of submarine current erosion. Part of the Carstone sequence in the Isle of Wight is also of *floridum* Subzone age. In the area to the north of Leighton Buzzard, Bedfordshire (Chamberlain Barn pit), the *regularis* and *kitchini* Subzones sediments were eroded and the debris redeposited during the *floridum* Subzone (Owen 1972).

Although there is a better representation of *floridum* Subzone times in the sedimentary sequence of the Anglo-Paris Basin when compared with earlier *chalensis* Zone sediments, and with a higher proportion of clay-grade clastics present, periods of strong current scour are well in evidence, particularly at the end of *floridum* Subzone times.

The Zone of *Otohoplites auritiformis* (new Zone)

Figs 36–38

In England and France, the genus *Otohoplites*, which is characteristic of the later Subzcnes of the *mammillatum* Superzone in the European faunal province, appears suddenly in the sedimentary sequence with only very rare transitional forms from *Pseudosonneratia* known. The development of the early species of *Otohoplites* inferred here is discussed later (pp. 220, 222) but it is considered to be a rapid event, analogous to the well represented but equally short-lived transitional phase between *Pseudosonneratia* (*Isohoplites*) and *Hoplites* which occurred at the end of the *mammillatum* Superzone. Bearing in mind that sediments of the *Otohoplites raulinianus* Subzone are very scattered in occurrence and, except in one instance, are strongly condensed by erosive submarine current action, it is not surprising that this transitional interval is barely represented.

The position of the '*larcheri*' Subzone of Destombes and the identity of *Otohoplites larcheri* has been discussed already (supra pp. 184–188). It is considered to fall within the early part of the *raulinianus* Subzone of Casey and herein. As yet, *Otohoplites auritiformis* Spath, the zonal index fossil proposed here, has not been found in these early sediments but certainly occurs within the strictly *raulinianus* Subzone pebble faunas elsewhere. *O. auritiformis* occurs also in the succeeding *Protohoplites* (*Hemisonneratia*) *puzosianus* Subzone and also in the *Otohoplites bulliensis* Subzone, but not typically in the terminal Subzone of *Pseudosonneratia* (*Isohoplites*) *steinmanni*. The *auritiformis* Zone is, therefore, an assemblage Zone and not strictly a total range Zone, but there is no chance of misidentification of sediments in this age in the European province on these grounds.

Otohoplites sinzowi Savel'ev has been used by its author as a Zone index for the equivalents of the *puzosianus* (*suborientalis*) Subzone and the *bulliensis* (*crassus*) Subzone. *O. sinzowi* is regarded here (supra p. 193) as falling within the range of morphological variation shown by *O. auritiformis* comparable to those variants which occur in the *bulliensis* Subzone deposits of France. The status of Destombes' Zone of *O. raulinianus* has been discussed previously (supra p. 190) and requires no further discussion here.

Figs 36–38 *Otohoplites auritiformis* (Spath). Later *mammillatum* Superzone index fossil. All × 1.

Figs 36a, b Partly phosphatized indigenous example figured by Casey (1960–, pl. LXXXV, fig. 1) as *Otohoplites glyphus*. Bed 33 (*puzosianus* Subzone fauna), Gault–Lower Greensand Junction Beds, near Copt Point, Folkestone, Kent. BGS Zk 4439, R. Casey Coll.

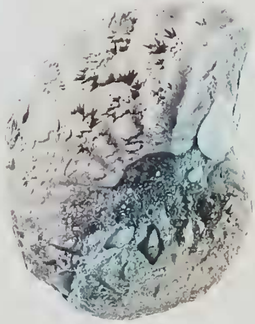
Figs 37a, b Wholly septate nucleus of an early form, BMNH C69868 Author's Coll., Bed 33 (ex *raulinianus* Subzone debris), same Member and locality as Fig. 36.

Figs 38a, b Copy of the original figures of the holotype of *Otohoplites sinzowi* Savel'ev (1973*b*, pl. 24, figs 4a–c), *crassus* Subzone, Mangyschlak.


36a


36b


37a


37b


38a


38b


38c

Subzone of *Otohoplites raulinianus* (Casey 1961)
Figs 39a, b

The *Otohoplites raulinianus* Subzone was recognized by Casey (1961) and deposits of this age in England have been described by him with additions by the author (Owen 1972). The subzonal index ammonite *O. raulinianus* (d'Orbigny) ranges in age from the base of the Subzone into the overlying *puzosianus* Subzone. *Otohoplites waltoni* Casey, the other characteristic species of *Otohoplites* occurring in the *raulinianus* Subzone, also ranges into the *puzosianus* Subzone, but both *O. raulinianus* and *O. waltoni* are uncommon in *puzosianus* Subzone deposits in England, and in the Boulonnais and Ardennes regions of France. The absence of the characteristic species of *Protohoplites* (*Protohoplites*) and *P.* (*Hemisonneratia*) of the *puzosianus* Subzone in deposits of *raulinianus* Subzone age, together with the other species of *Otohoplites* listed in Table 6 (pp. 208–211), precludes the possibility of confusion.

Sediments of the *raulinianus* Subzone are of very scattered occurrence, when present are usually highly condensed, and are often absent altogether. Only in the Bois de Perchois, Aube, is the Subzone known to be represented by uncondensed sediment which Destombes (1979) classified with his *O. larcheri* Subzone (supra pp. 184–190). In England, the fauna of this Subzone occurs free of admixture with other Subzones only in the sections exposed in north-west Kent (Casey 1961) and in the area north of Leighton Buzzard, Bedfordshire (Owen 1972). At Folkestone, Kent, the phosphatic pebble fauna of *raulinianus* Subzone age is mixed with that derived from the *floridum* Subzone and both are redeposited in sediments of early *puzosianus* Subzone age. At Wrecclesham, Surrey, there is a similar admixture of the pebble faunas derived from the former *floridum* and *raulinianus* Subzones deposits. In the Mangyschlak region of the Soviet Union, no ammonites of *raulinianus* Subzone age have yet been recorded and the lithological section suggests a non-sequence at the base of the *suborientalis* Subzone of Savel'ev (1973*a*).

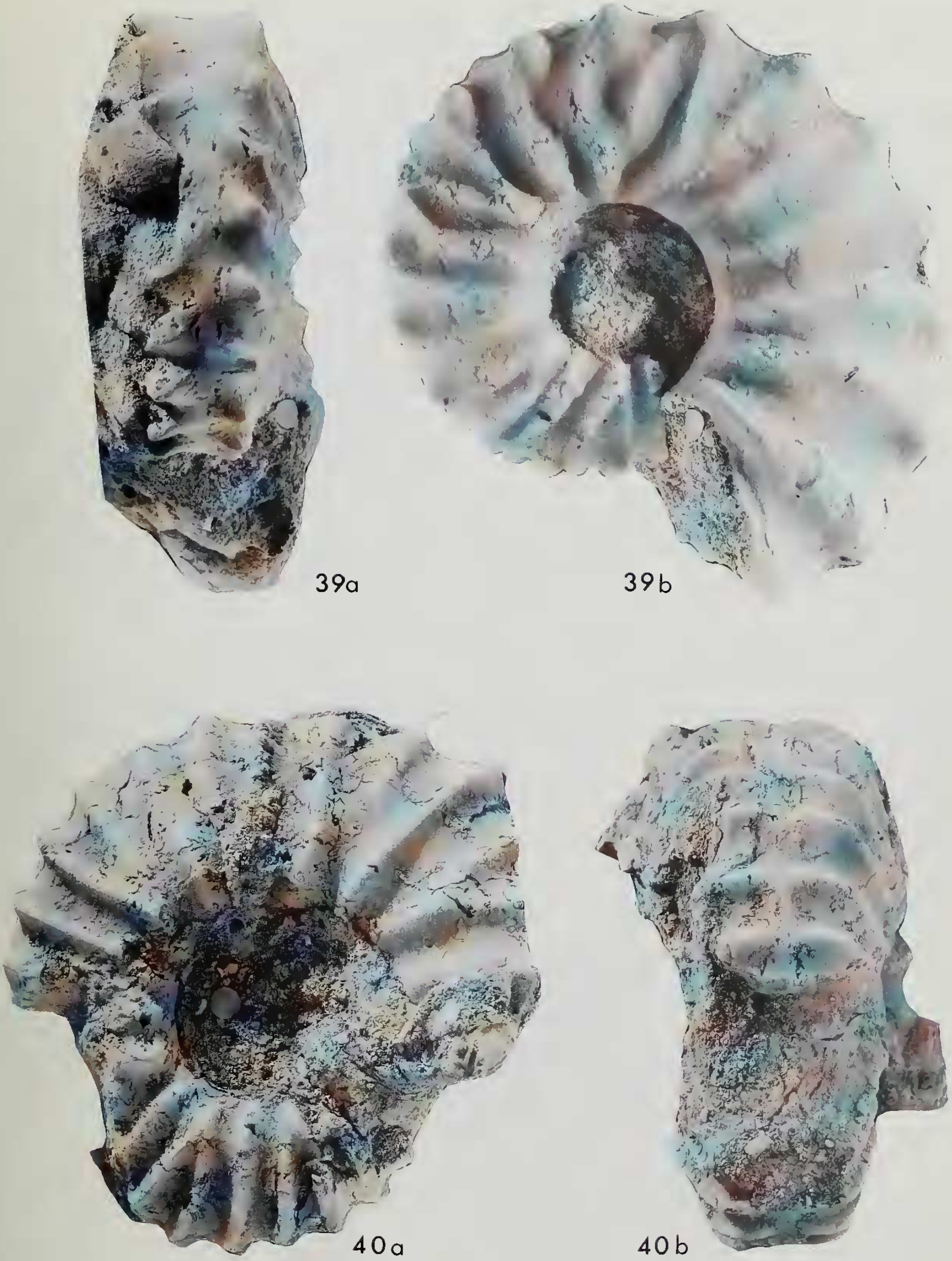
It could be argued that the *raulinianus* Subzone should be combined with the *puzosianus* Subzone. At present, it is desirable to separate those sediments in which the characteristic *puzosianus* Subzone fauna is absent, but which contains the early species of *Otohoplites*. The imperfect development of sediments of this age is due to a marked period of strong submarine current erosion which is geographically extensive in the European province. It precedes a more settled period of sedimentation which occurred during the latter part of the *mammillatum* Superzone.

Subzone of *Protohoplites* (*Hemisonneratia*) *puzosianus* (Casey 1961)
Figs 40a, b

This time interval is a total range Subzone of *P.* (*H.*) *puzosianus* (d'Orbigny). It could have been indexed equally with a species of *Protohoplites* (*Protohoplites*), such as *P.* (*P.*) *latisulcatus* (Sinzow) which has a very wide geographical distribution in sediments of this age in the European province. The genus is restricted to this Subzone. Savel'ev (1973*b*, 1974) has used *Tetrahoplites suborientalis* Savel'ev as an index for this interval of time in the Mangyschlak sequence. However, *Tetrahoplites* is very rare in western Europe as Casey has demonstrated (1960–, 471–6).

The *puzosianus* Subzone is well represented in the sedimentary sequence in western Europe and in Mangyschlak. At Folkestone, Kent, it is represented by the 'indigenous' fauna of the matrix of Bed 33 of Casey (1961, 528–31), the main *mammillatum* bed, and in overlying sediments up to and including the 'Sulphur Band', his Bed 35. Elsewhere in Kent and Surrey, the *puzosianus* Subzone sequence is widely represented by phosphatic nodule beds. At certain localities, such as Ford Place pit, Trottiscliffe, Kent, indigenous partly crushed and partly phosphatized fossils occur in sediments belonging to this Subzone.

In France, the *puzosianus* Subzone is represented at Wissant (Owen 1971, 82), and in the Ardennes (e.g. Amédro & Destombes 1975) where the main concentration of nodules at Machéroménil belongs to this Subzone. Elsewhere in France, deposits of *puzosianus* Subzone age have not yet been proved. The record of *puzosianus* Subzone sediments in the sequence exposed in the Bois de Perchois, Aube (Destombes 1979) is incorrect (supra pp. 184–190).



Figs 39–40 *Otohoplites auritiformis* Zone subzonal indices (part). All × 1.

Figs 39a, b *Otohoplites raulinianus* (d'Orbigny), early form BGS GSM 70474 R. Casey Coll. Bed 33 (ex *raulinianus* Subzone debris), Gault–Lower Greensand Junction Beds, near Copt Point, Folkestone, Kent.

Figs 40a, b *Protohoplites* (*Hemisonneratia*) *puzosianus* (d'Orbigny) BMNH C72831 Author's Coll., Bed 7 (Casey 1961), Ford Place pit, near Trottiscliffe, Kent.

In the Soviet Union, the sediments included by Savel'ev (1973*a*, 1974) in his Subzone of *Tetrahoplites suborientalis* contains a closely similar fauna to that of the *puzosianus* Subzone of western Europe.

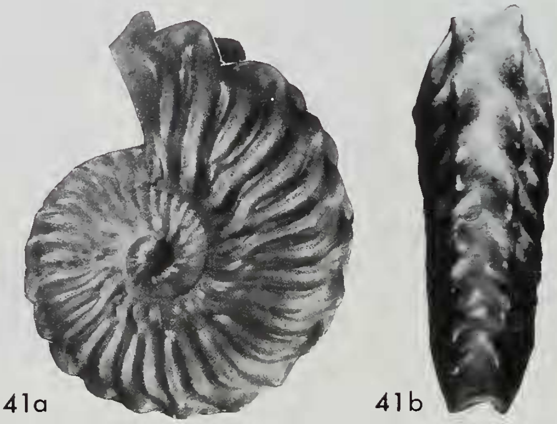
Subzone of *Otohoplites bulliensis* (Destombes 1973)
Figs 41a, b

The total range Subzone of *O. bulliensis* Destombes is well represented by clay sediments in the northern Pays de Bray and by glauconitic loams in the Aube (supra pp. 188–190). In England, the Subzone has not yet been proved unequivocally in the sedimentary sequences. However, between Sevenoaks, Kent, and Oxted, Surrey, there are poorly fossiliferous sediments intervening between proven deposits of *puzosianus* and *steinmanni* age which might prove positively to be of *bulliensis* Subzone age.

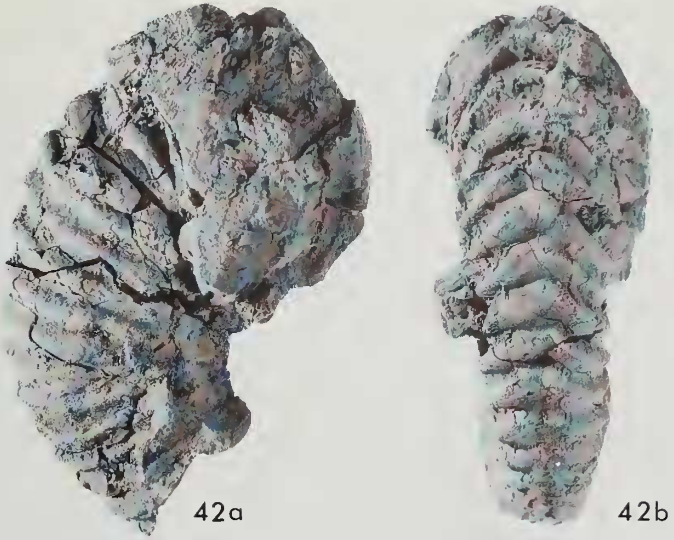
The Subzone is characterized by species of *Otohoplites* which possess a distinctly *Dimorphoplites*-like appearance. Prior to the work of Destombes, earlier accounts of the stratigraphy of sediments of this age actually record the presence of *Dimorphoplites*. Spath (e.g. 1942, 689, 733) was equally misled when revising the ammonite fauna described by Sinzow (1909) from Mangyschlak. He renamed a species of *Otohoplites*, now known to occur in the *bulliensis* Subzone, as *Dimorphoplites subhilli* (Spath 1942, 689). Sediments of *bulliensis* Subzone age are well developed in the Mangyschlak region where they have been grouped into a Subzone of *Otohoplites crassus* by Savel'ev (supra pp. 191, 193). The clays which contain species of *Otohoplites* recorded from the Schacht Konrad 1 borehole sequence in the Harz foredeep region of north Germany, below sediments of *steinmanni* age (Owen 1979, 568–9), may also belong to the *bulliensis* Subzone.

Subzone of *Pseudosonneratia* (*Isohoplites*) *steinmanni* (Casey 1961 emended)
Figs 42a, b

Casey (1961) used his species *Hoplites* (*Isohoplites*) *eodentatus* as the index for this unit of relative time, but his species is conspecific with *Pseudosonneratia* (*Isohoplites*) *steinmanni* (Jacob) (supra p. 195). Formerly the basal Subzone of the *Hoplites dentatus* Zone (Middle Albian), it is now regarded as the terminal Subzone of the *mammillatum* Superzone (Owen 1984, 1985). The *P.* (*I.*) *steinmanni* Subzone is a total range Subzone with an ammonite fauna still predominantly of *mammillatum* Superzone aspect, although foreshadowing that of the Middle Albian Subzone of *Lyelliceras lyelli*. At the end of *steinmanni* Subzone time, species of *Pseudosonneratia*



Figs 41a, b *Otohoplites bulliensis* Destombes, subzonal index fossil of the *bulliensis* Subzone. Copy of the original figure of the holotype (Destombes 1973, pl. 1, 1a), Bed 4a, Carrière Ledoigt, St Martin l'hortier, Pays de Bray.



Figs 42a, b *Pseudosonneratia* (*Isohoplites*) *steinmanni* (Jacob), subzonal index fossil of the *steinmanni* Subzone. BMNH C76480 Author's Coll. figured in Owen (1971, pl. 2, figs 1a, b) as *Hoplites* (*Isohoplites*) *eodentatus* Casey, Bed 1, Coney Hill sand pit, Tandridge, Surrey.

(*Isohoplites*) show an instability in the ventral arrangement of the rib pattern, which changes from the earlier isometric pattern across the venter to the en-echelon arrangement of the rib terminations across the venter and complete siphonal effacement typical of *Hoplites*. At the same time the lyelliceratid genus *Tegoceras*, typical of the later half of the *mammillatum* Superzone, developed clavi on ribs which changed from an en-echelon arrangement each side of the ventral region to the isometric arrangement characteristic of *Lyelliceras*.

The occurrence of deposits of *steinmanni* Subzone age in the Anglo-Paris Basin have been described by the writer (Owen 1971) with additional information by Destombes (1973, 1977*a*) and Amédro (1984*b*). The most complete sequence yet known is exposed in the Briqueterie Ledoigt, St Martin l'hortier (Bully) in the Pays de Bray, where the clays and the ammonite fauna have been described by Destombes (1973, 1977*a*). Apart from the occurrences of deposits of this Subzone in England and France, it is also known to be of widespread occurrence throughout the European province. Important sequences are known in Spitzbergen (Nagy 1970) where there is an admixture of ammonites of the Arctic genus *Grycia* including *G. sablei* (Imlay). Deposits of this Subzone are known to be present in the Schacht Konrad 1 clay sequence north of Salzgitter, north Germany (Owen 1979, 570), and eastwards in Poland (e.g. Marcinowski & Wiedmann 1985) and the Soviet Union (e.g. Savel'ev 1981).

Systematic Palaeontology

Stratigraphical distribution of the ammonite fauna

The ammonite fauna of the *mammillatum* Superzone so far described from western Europe is tabulated and arranged stratigraphically in Table 6. Savel'ev (1974, 1976) has listed an extensive fauna from the sequence exposed in the Mangyschlak Peninsula, but many of his species still remain to be monographed. Known occurrences of Russian species in western Europe are included in Table 6 and, where it is considered that these are synonymous with species described in western Europe, priority of nomenclature is discussed in the Systematic Notes.

The list in Table 6 is not simply a compilation of the extensive work of Casey (1960–) and Destombes (e.g. 1979). Apart from the changes made necessary by the revised subzonal arrange-

Table 6 Stratigraphical distribution of ammonites known to occur in specific Subzones in western Europe.

Subzones are numbered consecutively: (1) *perinflata*, (2) *kitchini*, (3) *floridum*, (4) *raulinianus*, (5) *puzosianus*, (6) *bulliensis*, (7) *steinmanni*. Number shown thus (**12**) in the list refer to the systematic section following this Table.

	chalensis			*auritiformis*			
	1	2	3	4	5	6	7
Hamitidae							
Hamites (*Hamites*) *pseudattenuatus* Casey	X		X				
„ „ *dixoni* Casey				X			
„ „ *hybridus* Casey				X			
„ „ *praegibbosus* Spath				X			
Anisoceratidae							
Protanisoceras (*Protanisoceras*) *actaeon* (d'Orbigny)			X				
„ „ *blancheti* (Pictet & Campiche)			X			X	
„ „ *cantianum* Spath			X	X	X		
„ „ *hengesti* Casey			X		?		
„ „ *major* Casey			X				
„ „ *vaucherianum* (Pictet)			X		X	X	
„ „ *coptense* Casey				X			
„ „ cf. *halleri* (Pictet & Campiche)				X			
„ „ *lardyi* (Pictet & Renevier)				X			
„ „ *raulinianum* (d'Orbigny)				X	X		
„ „ *subquadratum* Casey				X			
„ „ *ventrosum* Casey				X			
„ „ *moreanum* (Buvignier)							X
„ „ spp.						X	X
„ (*Torquistylus*) *anglicum* Spath				X			
Rossalites albini Destombes			X				
„ *oweni* Casey					X		
Astiericeratidae							
Astiericeras astierianum (d'Orbigny)							X
Beudanticeratinae (Desmoceratidae)							
Beudanticeras arduennense Breistroffer	X	X	X	X	X	X	
„ *dupinianum* (d'Orbigny)	X		X	X	X	X	
„ „ *evolutum* Casey				X			
„ *newtoni* Casey		X	X	X	X	X	
„ *perchoisense* Destombes			X				
„ *bulbosum* Casey				X			
„ *laevigatum* (J. de C. Sowerby)					X	X	X
„ *albense* Breistroffer						X	X
„ *sanctaecrucis* Bonarelli							X
Uhligella subornata Casey				X			

Table 6 continued

	chalensis			*auritiformis*			
	1	2	3	4	5	6	7
Douvilleiceratinae (Douvilleiceratidae)							
Douvilleiceras leightonense Casey	X	X					
„ „ *pringlei* Casey		X	X				
„ *mammillatum* (Schlotheim)			X	X	X	X	
„ „ *aequinodum* (Quenstedt)	X	X	X(1)	X	X		
„ „ *praecox* Casey			X	X	X		
„ *orbignyi* Hyatt		X		X	X	X	X
„ *pustulosum* Casey		X	X				
„ *alternans* Casey			X(2)	X	X		
„ *magnodosum* Casey			X(3)				
„ *scabrosum* Casey			X	X	X		X
„ *monile* (J. Sowerby)				X		X	
„ *inaequinodum* (Quenstedt)							X
Cleoniceratinae (Cleoniceratidae)							
Anadesmoceras baylei (Spath)		X					
Cleoniceras (*Cleoniceras*) *strigosum* Casey	X						
„ „ *morgani* Spath		X					
„ „ *cleon* (d'Orbigny)			X				
„ „ *dimorphum* Casey			X				
„ „ (4) *floridum* Casey			X(5)				
„ „ *janneli* (Parent)			X(6)	X			
„ „ *renatae* Mirzoyev			X				
„ „ *seunesi* Bonarelli			X	X			
„ „ *sublaeve* Casey			X				
„ „ *mocqueryi* Destombes				X			
„ „ *quercifolium* (d'Orbigny)				X	X		
„ „ *devisense* Spath							X
„ „ spp.						X	
„ (*Neosaynella*) *cantianum* Casey			X				
„ „ *inornatum* Casey			X				
„ „ aff. *platydorsatum* (Sinzow)			X				
„ „ spp.						X	
Lemuroceratinae (Cleoniceratidae)							
Cymahoplites? sp.				X			
Sonneratiinae (Hoplitidae)							
Sonneratia (*Globosonneratia*) *perinflata* Breistroffer	X(7)						
„ (*Sonneratia*) (8) *chalensis* Casey	X	X					
„ „ *flava* Casey			X				
„ „ *elegans* Casey		X					
„ „ *kitchini* Spath		X					
„ „ „ *ovalis* Casey		X					
„ „ *parenti* Jacob		X					
„ „ *rotator* Casey		X					
„ „ „ *solida* Casey		X					
„ „ „ *leightonense* Casey		X					
„ „ *subglabra* Casey		X					
„ „ *caperata* Casey			X(9)				
„ „ *extremis* Casey			X				
„ „ *rotula* Savel'ev			X(10)				
„ „ *subsarasini* Destombes			X				
„ „ *vnigri* Savel'ev			X(11)				
„ „ *trigonalis* Casey				X			
„ „ *dutempleana* (d'Orbigny)					X		

Table 6 continued

	chalensis			*auritiformis*			
	1	2	3	4	5	6	7
Pseudosonneratia (*Pseudosonneratia*) **(12)** *crassa* Casey			X		X		
„ „ *flexuosa* Destombes			X				
„ „ *jacobi* Casey			X		X		
„ „ *palaeodentata* Destombes			X				
„ „ *typica* Spath					X		
„ (*Isohoplites*) **(12)** *acuta* Casey					X		
„ „ *occidentalis* Casey					X		
„ „ „ *pluricostata* Casey					X		
„ „ *praedentata* Casey					X		
„ „ *iserensis* Spath			X		X		
„ „ *laffrayei* Breistroffer							X
„ „ *steinmanni* Jacob							X(13)
„ „ spp.							X
Tetrahoplites dragunovi Savel'ev					X		
„ *orientalis* Casey					X		
„ *suborientalis* Savel'ev					X		
„ *subquadratus* (Sinzow)					X		
Otohoplites auritiformis (Spath)				X	X	X(14)	aff.
„ „ *planidorsatus* Casey					X		
„ *elegans* (Spath)				X	X		
„ *icarus* Casey				X			
„ *polygonalis* Casey				X	X		
„ *raulinianus* (d'Orbigny)				X(15)	X	aff.	
„ *subguersanti* Casey				X			
„ *waltoni* Casey				X(15)	X	aff.	
„ „ *niger* Casey				X	aff.		
„ *destombesi* Casey					X	X	
„ *guersanti* (d'Orbigny)					X		
„ „ *semiglabrus* Casey					X		
„ *involutus* Casey					X		
„ *maxinae* Casey					X		
„ *oweni* Casey					X		
„ *simplex* Casey					X		
„ *subchloris* Casey					X		
„ *bulliensis* Destombes						X	
„ *crassus* Savel'ev						X	
„ *normanniae* Destombes, Juignet & Rioult							X
„ „ *compressa* Destombes, Juignet & Rioult							X
„ „ *inflata* Destombes, Juignet & Rioult							X
„ *subhilli* (Spath)					?	X(16)	
„ *cunningtoni* (Spath)							X
„ spp.							X
Hoplites caletanus Destombes, Juignet & Rioult							X
„ spp. immediate forerunners of *H. bullatus* and *H. dentatus*							X
Anahoplitoides gigas (Sinzow)			X(17)				**(18)**
Protohoplites (*Protohoplites*) *archiacianus* (d'Orbigny)					X		
„ „ *latisulcatus* (Sinzow)					X		
„ „ *michelinianus* (d'Orbigny)					X		
„ „ „ *costatus* Casey					X		
„ (*Hemisonneratia*) *cantianus* Casey					X		
„ „ *gallicus* (Breistroffer)					X		
„ „ *puzosianus* (d'Orbigny)					X		

Table 6 continued

	chalensis			*auritiformis*				
	1	2	3	4	5	6	7	
Gastroplitinae (Hoplitidae) **(19)**								
Sokolovites sp.						X		
Engonoceratidae								
Parengonoceras ebrayi (de Loriol)			X					
Platyknemiceras sequanense Destombes			X					
Lyelliceratinae (Lyelliceratidae)								
Tegoceras gladiator (Bayle)			X	X	X			
„ „ *attenuata* Destombes				X				
„ „ *evoluta* Destombes				X				
„ *miles* Casey				X				
„ *mosense* (d'Orbigny)					X			
„ *quadratum* Destombes						X		
„ *camatteanum* (d'Orbigny)							X	
„ *vaasti* Destombes, Juignet & Rioult							X	
„ –*Lyelliceras* transitional spp.								X **(20)**
Mojsisovicsiinae (Mojsisovicsiidae) **(21)**								
Oxytropidoceras alticarinatum (Spath)				X				
Brancoceratinae (Brancoceratidae) **(22)**								
Parabrancoceras spp.							X	

ment, additional information is included. This list supersedes, therefore, the ammonite faunal lists produced by Kennedy & Hancock (1978, v5–v6). The numbers in brackets in Table 6 refer to specific notes in the systematic section of this paper which follows.

Systematic Notes

Suborder **AMMONITINA** Hyatt, 1889

Superfamily **DOUVILLEICERATACEAE** Parona & Bonarelli, 1897

Family **DOUVILLEICERATIDAE** Parona & Bonarelli, 1897

Subfamily **DOUVILLEICERATINAE** *sensu stricto*

Genus ***DOUVILLEICERAS*** de Grossouvre, 1893

TYPE SPECIES. *Ammonites mammillatus* Schlotheim (ICZN Opinion 422).

DISCUSSION. A number of the specimens of *Douvilleiceras* described and figured by Destombes (1979) are considered here to have been misidentified and to fall closely within the range of variation shown by previously established species or subspecies.

(1). *Douvilleiceras perchoisense* Destombes (1979, 72–3; pl. 4–4, figs 2a, b) is close, morphologically, to *Douvilleiceras mammillatum aequinodum* (Quenstedt) figured by Casey (1960–, 272, text-fig. 94a–c). The specimens figured by Destombes as *D. mammillatum aequinodum* (1979, pl. 4–4, figs 1a, b; pl. 4–5, figs 2a, b) are within the range of morphology shown by *D. mammillatum praecox* Casey (1960–, 272–3, text-figs 94d, e; pl. XLI, figs 8a, b).

(2). The specimen figured by Destombes (1979, pl. 4–5, fig. 1; pl. 4–6, fig. 1) as *Douvilleiceras orbignyi* Hyatt, is conspecific with *Douvilleiceras alternans* Casey (1960–, 282; pl. XLII, figs 1a, b).

(3). The specimen figured by Destombes (1979, pl. 4–6, figs 2a, b) as *Douvilleiceras inaequinodum* (Quenstedt) is very close, morphologically, to the contemporary *floridum* Subzone species *D. magnodosum* Casey (1960–, 284; pl. XLII, figs 4a, b) which, although possessing exaggerated ventrolateral tubercles, is otherwise distinct from the later *D. inaequinodum* as Casey has already recognized.

Superfamily **HOPLITACEAE** Douvillé, 1890 (ICZN Opinion 353)

Family **CLEONICERATIDAE** Whitehouse, 1926

INTRODUCTION. This family has been the subject of considerable revision in the past, with the homoeomorphic Aptian forms included in it originally by Whitehouse being eliminated, and the family reduced in status to that of a subfamily within the Hoplitidae (Wright 1957 Treatise, L394; Casey 1960–, 548–53; Savel'ev 1973*a*; Wright 1981, 169). However, much more of the early history of *Cleoniceras*, the nominate genus, is now known. It is apparent that the supposed direct relationship between the Cleoniceratinae and the Hoplitinae envisaged by Casey does not exist. The supposed phylogenetic arrangement and dating of genera grouped within the Cleoniceratinae and Vnigriceratinae by Savel'ev (1973*a*, fig. 10), both included in Hoplitinae by Wright (1981), require substantial revision. The present evidence indicates an origin of several cleoniceratid stocks in the early to mid-*tardefurcata* Zone genus *Freboldiceras* which in turn is linked with the Desmoceratidae, as is the Hoplitinae. However, *Freboldiceras* has an origin in the Subfamily Puzosiinae, whereas the Hoplitinae originate in the Beudanticeratinae. It is necessary, therefore, to separate the Cleoniceratidae from the Hoplitidae and to recognize three subfamilies; the Cleoniceratinae *sensu stricto* which corresponds closely to the definition of it given by Wright (1957) and Casey (1960–), the Vnigriceratinae Savel'ev 1973 emended herein and the Lemuroceratinae nov. for the separate offshoot which produced *Lemuroceras*, *Cymahoplites* and *Puzosigella*.

DIAGNOSIS. Discoidal to compressed moderately involute shells with subrectangular to high whorl-sections showing subtabulate arched to acute venters and a tendency to produce scaphitoid body chambers. Ornament consists of feeble to strongly developed sigmoid to falcoid ribs with constrictions in some genera. The ribbing stems from comma-shaped bullae projected from the umbilical margin high onto the whorl flank particularly in earlier genera. Ribs arise in pairs or triplets from these elongated bullae and are projected forward isometrically across the venter with some effacement along the siphonal line. In genera with subtabulate venters, some thickening of the ribs occurs at the ventrolateral shoulders, but these are never tuberculate. Suture line with first lateral saddle and lobe wide, tendency to asymmetry or markedly asymmetric (Figs 43A–E).

DISCUSSION. The Cleoniceratidae encompasses genera of wide geographic distribution but which appear to have originated in the early Albian Arctic province genus *Freboldiceras* which,

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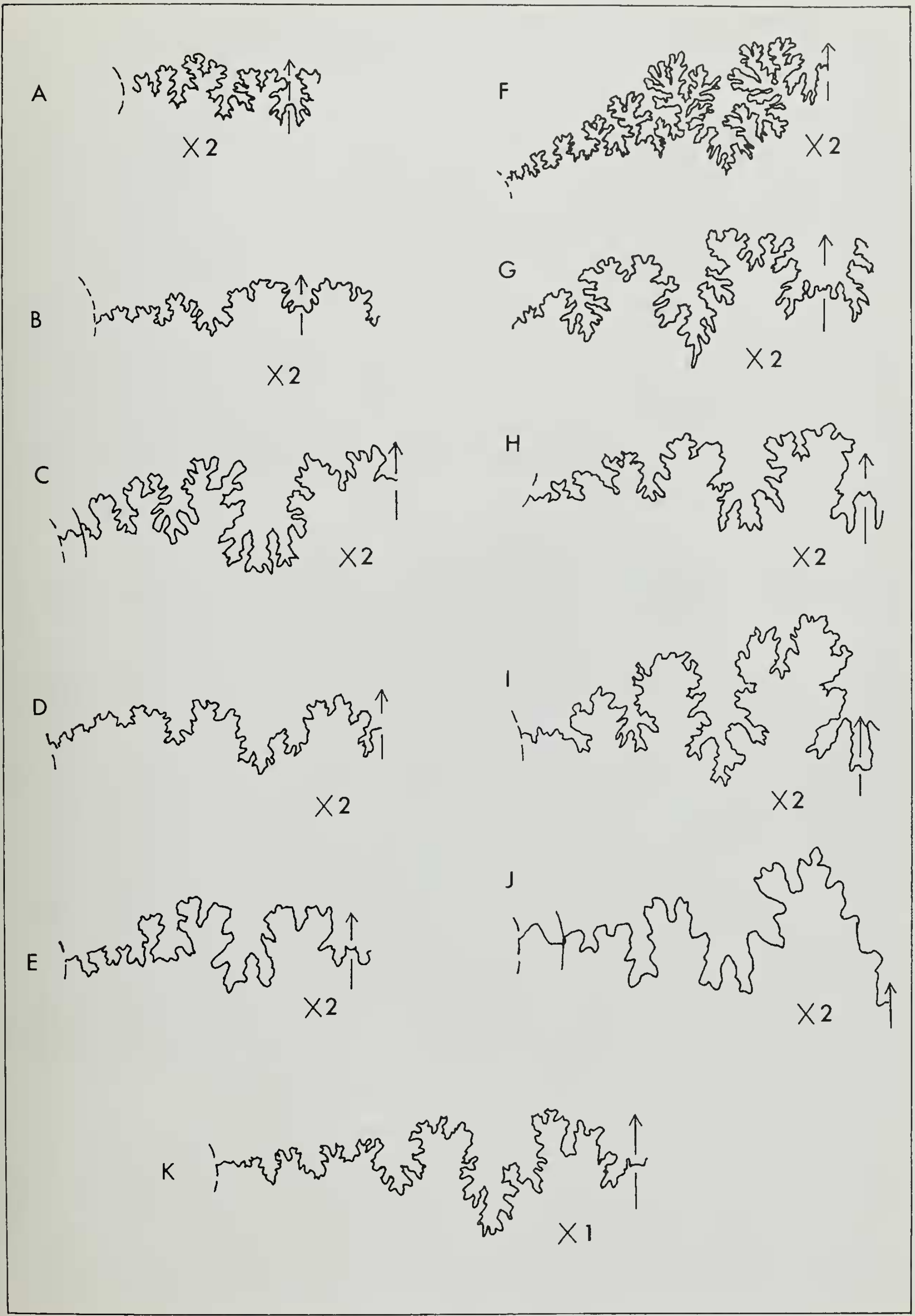
Fig. 43 External septal suture patterns.

A. *Puzosia alaskana* Imlay. After Imlay (1960, pl. 16, fig. 6) reversed.
B. *Arcthoplites birkenmajeri* Nagy, a transitional species from *Freboldiceras*. Copy of Nagy (1970, fig. 12d, reduced to × 2).
C. *Farnhamia farnhamensis* Casey. BMNH C84762 C. W. & E. V. Wright Coll., reversed.
D. *Cleoniceras* (*Cleoniceras*) *cleon* (d'Orbigny). Copy of Casey (1960–, 556, fig. 211h reduced to × 2).
E. *Lemuroceras aburense* (Spath). BMNH C51716 Besairie Coll., *mammillatum* Zone, Ambaramaninga, Madagascar.
F. *Beudanticeras beudanti* (Brongniart). Copy of Casey (1960–, 146, fig. 46c reduced to × 2).
G. *Sonneratia trigonalis* Casey. Copy of Casey (1960–, 531, fig. 199a reduced to × 2).
H. *Otohoplites auritiformis* (Spath). BMNH C72255 Author's Coll. reversed.
I. *Hoplites dentatus* (J. Sowerby). BMNH C34839 Spath Coll. reversed.
J. '*Anahoplites*' *yakounensis* (Whiteaves). Geological Survey of Canada (GSC) 7594 McLearn Coll.
K. *Gastroplites canadensis* (Whiteaves). BMNH C53046 Spath Coll.


A
×2
B
×2
C
×2
D
×2
E
×2
F
×2
G
×2
H
×2
I
×2
J
×2
K
×1

in turn, appears to have an origin in *Callizoniceras* (*Callizoniceras*) (Puzosiinae). There is no evidence of a post-early *acuticostata* Subzone occurrence of *Freboldiceras* (cf. Savel'ev 1973*a*). Several developments occurred; the earliest being in the early part of the *acuticostata* Subzone (mid-*tardefurcata* Zone) where *Arcthoplites* developed directly from *Freboldiceras* (Birkelund & Håkansson 1983). *Arcthoplites* in turn gave rise to a number of closely related genera which lived during the *acuticostata* and *regularis* Subzones of the *tardefurcata* Zone and which are grouped here in the emended Subfamily Vnigriceratinae Savel'ev. The second development was the penecontemporaneous production of discoidal shells typified by the genus *Cleoniceras*. *Cleoniceras* appears in the *acuticostata* Subzone and might, like its contemporary in that Subzone *Anadesmoceras*, have developed from *Subarcthoplites* or *Bellidiscus* by a marked increase in whorl height. Equally, *Cleoniceras* may have developed independently from *Freboldiceras*. Once initiated, however, it is apparent that the Cleoniceratinae diverged from the Vnigriceratinae as interpreted here. The current view that the Gastroplitinae developed from the Cleoniceratinae (e.g. Jeletzky 1980) is not proven on the evidence now available. The various vnigriceratine genera formerly included in Gastroplitinae (e.g. Wright 1957), a Subfamily still regarded here as belonging in the Hoplitidae, are distinct from the genera *Lemuroceras*, *Cymahoplites* Spath *non* Casey and *Puzosigella* formerly also included in the Gastroplitinae or with question in the Cleoniceratinae. These three genera form a specialized *mammillatum* Superzone development grouped here in a separate new Subfamily Lemuroceratinae. Although they show affinity with the late *tardefurcata* Zone genus *Vnigriceras*, they may have an independent puzosiinid origin.

Subfamily **VNIGRICERATINAE** Savel'ev, 1973

INTRODUCTION. The Subfamily Vnigriceratinae was proposed by Savel'ev (1973*a*, 132–3) to include the genera *Anadesmoceras* Casey 1954, *Vnigriceras* (*Vnigriceras*) and *V.* (*Astrodiscus*) Savel'ev 1973, *Lemuroceras* Spath 1942, *Subarcthoplites* Casey 1954 (emended Imlay 1961), *Leconteites* Casey 1954, ?*Puzosigella* Casey 1954 and ?*Freboldites* (sic) Imlay 1959. With the improved knowledge of the age distributions and interrelationships of these genera together with the validity of the distinctions made by Savel'ev between Vnigriceratinae and Cleoniceratinae, a radical revision of his systematic conclusions has now to be made.

The Arctic province genus *Freboldiceras* Imlay 1959 was attached to the Vnigriceratinae with question by Savel'ev (1973*a*) and was considered to be a late *mammillatum* Superzone (*mangyschlakense* Zone) derivative of the genus *Subarcthoplites*. As indicated above, the genus *Arcthoplites* is closely related to penecontemporaneous *Freboldiceras* and, in turn, grades into *Subarcthoplites*, of which genus *Bellidiscus* Savel'ev 1973*a* is probably a synonym. The degree of revision required to Savel'ev's concept of the subfamily may be gained by noting that the true age of *Freboldiceras* is of the early *tardefurcata* Zone, *schrammeni* and *acuticostata* Subzones, and forms the root stock of the group of ammonite genera for which Vnigriceratinae has to be used. *Arcthoplites* was not included in the subfamily by Savel'ev and *Bellidiscus* was placed in the Cleoniceratinae despite the close relationship of the genus with *Subarcthoplites*. Conversely, *Anadesmoceras* was included by Savel'ev in Vnigriceratinae despite its close relationship with *Cleoniceras*. *Vnigriceras* and *Leconteites* of late *tardefurcata* Zone, *regularis* Subzone, age are probably congeneric. *Lemuroceras* and *Puzosigella* do not belong in Vnigriceratinae and are included with *Cymahoplites* Spath in a new subfamily Lemuroceratinae. The Vnigriceratinae defined here may be diagnosed as follows.

EMENDED DIAGNOSIS. Cleoniceratidae with well-rounded subquadrate to moderately high whorl sides and rounded, slightly flattened venters. Ornament of ribs stemming from comma-shaped bullae at the umbilical margin projected high onto the whorl flank. The ribs bifurcate irregularly at the ventrad end of each bulla and swing isometrically forward across the venter with some weakening in strength along the siphonal line. Some thickening of the ribs occurs at the ventrolateral shoulders. Whorl height on more evolute forms tends to increase with age and the ornament becomes strongly reduced. Constrictions may be present. Septal sutural configuration cleoniceratid.

DISCUSSION. The following genera are included here in this Subfamily: *Freboldiceras* Imlay 1959 (Type species *Freboldiceras singulare* Imlay); *Arcthoplites* Spath 1925 (Type species *Ammonites jachromensis* Nikitin); *Subarcthoplites* Casey 1954 (Type species *Lemuroceras belli* McLearn); *Bellidiscus* Savel'ev 1973*a* (Type species *Bellidiscus probus* Savel'ev); *Leconteites* Casey 1954 (Type species *Desmoceras lecontei* Anderson); *Vnigriceras* Savel'ev 1973*a* (Type species *Vnigriceras* (*V.*) *emendatus* Savel'ev) including Subgenus *Astrodiscus* Savel'ev 1973*a* (Type species *Vnigriceras* (*Astrodiscus*) *insegestus* Savel'ev). The genera comprising this Subfamily, known at present, are confined to the *Leymeriella tardefurcata* Zone (Owen 1988). All speculative *Douvilleiceras mammillatum* Superzone dates for *Freboldiceras* (e.g. Savel'ev 1973*a*) and *Arcthoplites* (e.g. Jeletzky 1980) are incorrect. The earliest genus to appear is *Freboldiceras*, which is associated in Peary Land, north Greenland, with *Leymeriella trollei* Birkelund & Håkansson of late *schrammeni* Subzone age (Birkelund & Håkansson 1983), and with *Leymeriella* of *acuticostata* Subzone age in west Spitzbergen (Nagy 1970). This genus is transitional from a puzosiinid ancestor, probably the late Aptian *Callizoniceras* (*Callizoniceras*), to *Arcthoplites* which is confined to the early part of the *acuticostata* Subzone in Spitzbergen and in the Soviet Union (the *tardefurcata* Zone of Savel'ev 1973*a*). *Subarcthoplites* and *Bellidiscus* are of *acuticostata* Subzone age and further study may show that they are inseparable at generic rank. The same may also prove to be the case with *Leconteites* and *Vnigriceras* which are of *regularis* Subzone age.

The genus *Farnhamia* Casey 1954 (Type species *Farnhamia farnhamensis* Casey) consists of a group of large ammonites from the Folkestone Beds of the Weald of south-east England. Casey (1960–, 465–71) recognized four contemporaneous species in sediments classified by him as being of an equivalent age to that of *Leymeriella schrammeni* in the north German sequence. The inner whorls indicate that these are species of *Arcthoplites* well within the range of variation shown by the species described by Savel'ev (1973*a*). The sediments containing '*Farnhamia*' are now correlated with the *acuticostata* Subzone of the classic German sequence (Owen 1988).

Subfamily **CLEONICERATINAE** Whitehouse 1926

DIAGNOSIS. Cleoniceratidae with discoidal to compressed, moderately involute shells and narrowly arched to acute venters showing a tendency to flatten along the siphonal line. Scaphitoid adult body chambers are present in some genera. Ornament of sigmoid to falcoid ribs stemming from comma-shaped bullae close to the umbilical margin, commonly bifurcating on the lower whorl flank and passing over the venter with a distinct forward projection and a tendency to effacement along the siphonal line. Constrictions are present in some genera and the ornament as a whole may be strongly developed or reduced to the point of smoothness.

DISCUSSION. The above diagnosis differs little from that of Wright (1957, L394) or that implied by Casey (1960–, 548–53). Their concept and that of Savel'ev, of an origin of this subfamily within *Uhligella* of the Desmoceratidae (Beaudanticeratinae), is not accepted here for the reasons stated above in connection with the origins of the Cleoniceratidae as a whole.

The genera included in the Subfamily here are: *Cleoniceras* Parona & Bonarelli 1897 (Type species *Ammonites cleon* d'Orbigny and including *Paracleoniceras* Collignon 1963 with Type species *Cleoniceras* (*Aioloceras*) *besairei* Collignon and *Cleonella* Destombes 1970 with Type species *Cleoniceras dimorphum* Casey as subjective synonyms) with subgenera *Neosaynella* Casey 1954 (Type species *Cleoniceras* (*Neosaynella*) *inornatum* Casey) and *Grycia* Imlay 1961 (Type species *Cleoniceras* (*Grycia*) *sablei* Imlay); *Anadesmoceras* Casey 1954 (Type species *Anadesmoceras strangulatum* Casey); *Anacleoniceras* Mirzoev 1969 (Type species *Anacleoniceras caseyi* Mirzoev); ?*Aioloceras* Whitehouse 1926 (Type species *Cleoniceras argentinum* Bonarelli).

Cleoniceras and *Anadesmoceras* appear in the *acuticostata* Subzone of the *tardefurcata* Zone in the Soviet Union (e.g. Savel'ev 1973*a*) and in contemporaneous deposits in the Arctic regions of North America (see Owen 1988). Both genera appear to have developed from the *Arcthoplites–Subarcthoplites/Bellidiscus* complex by the development of discoidal shells with high whorl sides. However, a direct derivation of *Cleoniceras* from *Freboldiceras* should not be discounted. *Anadesmoceras* does not appear to survive the end of the *tardefurcata* Zone. The *Cleoniceras* stock proliferates in the *Douvilleiceras mammillatum* Superzone to produce the subgenera *Neosaynella* and *Grycia* together with the genus *Anacleoniceras*. *Cleoniceras* (*Cleoniceras*) persists as a great rarity into the early Middle Albian (early *Lyelliceras lyelli* Subzone) in the European province.

Genus *CLEONICERAS* Parona & Bonarelli 1897

Type species. *Ammonites cleon* d'Orbigny 1850.

Discussion. The following subgenus and species described by Destombes are considered here to be synonyms with previously described forms.

(4). *Cleonella* Destombes (1970, 2062), with Type species *Cleoniceras* (*Cleoniceras*) *dimorphum* Casey, was proposed as a subgenus to include forms such as *C.* (*C.*) *floridum* Casey and *C.* (*Neosaynella*) *cantianum* Casey. *C.* (*C.*) *floridum* Casey cannot be separated at subgeneric rank from *Cleoniceras cleon* (d'Orbigny), the type species of *Cleoniceras*. *C.* (*N.*) *cantianum* Casey is a true *Neosaynella*. *C.* (*C.*) *dimorphum* Casey is morphologically midway between the subgenera *Cleoniceras* and *Neosaynella* and the use of the subgeneric concept *Cleonella* is considered to be unnecessary here.

(5). *Cleoniceras* (*Cleonella*) *lanceolatum* Destombes (1979, 94–5; pl. 4–16, figs 1a, b, 2a, b) is considered here to fall within the morphological variation shown by *Cleoniceras* (*Cleoniceras*) *floridum* Casey (e.g. Casey 1960–, 566–8; pl. XCII, figs 1a, b, 5, 7 and many specimens in collections from sections in the Weald of southeast England).

(6). *Cleoniceras* (*Cleonella*) *ornatum* Destombes (1979, 94; pl. 4–16, figs 6a, b) is indistinguishable from *Cleoniceras* (*Cleoniceras*) *janneli* (Parent).

Subfamily **LEMUROCERATINAE** nov.

Diagnosis. Cleoniceratidae with evolute to moderately involute discoidal shells with flattened to gently concave, high whorl sides and tabulate to rounded venters. Ornament consisting of primary ribs arising from faint comma-shaped elongated bullae close to the umbilical margin, bifurcating above the bullae, with occasional secondary ribs arising directly at the umbilical margin. Ribs are sigmoid to gently falcoid on whorl flanks and continue with a variable amount of effacement across the venter. Ornament becomes markedly reduced in the adult shell.

Discussion. In his *Monograph of the Ammonoidea of the Lower Greensand*, Casey discussed the genus *Cymahoplites* twice (1960–, 165–9, 550–1). His earlier reading of this genus in 1961 is followed here. However, in his later account in 1966, he included within *Cymahoplites* species of *tardefurcata* Zone age which are now regarded as belonging to *Vnigriceras*. By so doing, he materially altered his concept of *Cymahoplites*. At present, *Cymahoplites* is known only with any certainty from the early part of the *mammillatum* Superzone and is of about the same age as the Tethyan province genus *Lemuroceras*. The age of the *Lemuroceras* fauna has been placed by Collignon (1978, xv13) well within the Middle Albian, but this reading is incorrect. The age of the fauna is earlier than that of the basal Middle Albian Subzone of *Lyelliceras lyelli* and is associated in India with early *mammillatum* Superzone species of *Douvilleiceras*. The fauna is earlier, therefore, than the late Lower Albian date suggested by Kennedy (1985, 94). *Cymahoplites* and the penecontemporaneous *Lemuroceras* appear to be a specialized cleoniceratid offshoot with a possible origin in *Vnigriceras* and with no known successors. A separate derivation from Puzosiinae is also possible. *Puzosigella* (Casey 1954) appears to be the Pacific province representative of this stock.

The following genera are included here in the Lemuroceratinae: *Lemuroceras* Spath 1942 (Type species *Pseudohaploceras aburense* Spath), *Cymahoplites* Spath 1922 (Type species *Ammonites kerenskianus* Bogoslowsky), and *Puzosigella* Casey 1954 (Type species *Pachydiscus sacramenticus* Anderson).

Family **HOPLITIDAE** Douvillé 1890 (Boehm 1895)

DISCUSSION. The family Hoplitidae is considered here to comprise three subfamilies; the Sonneratiinae Destombes, Juignet & Rioult 1973 emended herein, the Hoplitinae *sensu stricto* (to include also the Schloenbachiidae Parona & Bonarelli 1897) and, with question, the Gastroplitinae Wright 1952 emended herein. This interpretation of the Family differs significantly from that of Wright (1981) who, like earlier authors, includes cleoniceratine elements with a puzosiinid ancestry in Hoplitidae which has an origin in the Beudanticeratinae, so making the Family polyphyletic. As now restricted, the Hoplitidae commences with the Sonneratiinae, which is a *mammillatum* Superzone development of closely related genera with an origin in the Beudanticeratinae, and possibly within the genus *Uhligella*, as envisaged by Spath (1942), Casey (1954; 1960–, 462–3) and Wright (1957; 1981). The Hoplitinae, as interpreted here, is derived from *Pseudosonneratia* (*Isohoplites*) during the late *auritiformis* Zone, *steinmanni* Subzone, continuing through the Middle and Upper Albian into the Cenomanian where it is represented by the genus *Schloenbachia*, a derivative of the late Albian genus *Callihoplites*. The Family grouping Schloenbachiidae of Parona & Bonarelli should be included in the synonymy of the Hoplitinae Douvillé. The third Subfamily included here with question is the Gastroplitinae which appears to have an origin in the *auritiformis* Zone genus *Sokolovites* which, in turn, is closely related to the Sonneratiinae as interpreted here.

Subfamily **SONNERATIINAE** Destombes, Juignet & Rioult 1973 emended

INTRODUCTION. The Subfamily Sonneratiinae was proposed by Destombes, Juignet & Rioult (1973, 70) to include the following genera: *Bucaillella* Destombes, Juignet & Rioult 1973, *Farnhamia* Casey 1954, *Sonneratia* Bayle 1878, *Tetrahoplites* Casey 1952, *Tetrahoplitoides* Casey 1954, *Pseudosonneratia* Spath 1925, *Protohoplites* (*Hemisonneratia*) (Breistroffer) Casey 1952 and *Protohoplites* (*Protohoplites*) Spath 1923. As such, this taxon includes forms like *Bucaillella* of ?upper Aptian age, *Farnhamia* which is considered here to be inseparable from *Arcthoplites* belonging to the Cleoniceratidae (Vnigriceratinae), and *Tetrahoplitoides* of late *tardefurcata* or *mammillatum* Superzone age, none of which are related to *Sonneratia* or its descendants. Moreover, this Subfamily was included in the synonymy of the Cleoniceratinae by Wright (1981) which, as has been discussed above, has a separate *tardefurcata* Zone origin ultimately in the Puzosiinae. If grouping at subfamily level is to have any phylogenetic meaning at all, as opposed to a mere collection of shapes, the Sonneratiinae and to a lesser extent the Hoplitinae require to be extensively revised. The Subfamily Sonneratiinae may be defined as follows.

DIAGNOSIS. Hoplitidae with moderately involute to evolute shells, showing subquadrate rounded to moderately high whorl sections with flattened sides and a strongly developed ornamentation of ribs which end in ventrolateral tubercles in some genera. The ribs arise, usually by bifurcation, from bullae at the umbilical margin, although single ribs or trifurcation can occur. The ribs describe an arcuate to sigmoid line on the whorl flank and, in genera such as *Sonneratia* and *Pseudosonneratia*, sweep across the venter in blunt, forward-directed chevrons with a tendency to effacement along the siphonal line in some forms. Ribbing in offshoots of this conservative stock, such as *Protohoplites* and *Otohoplites*, exhibit effacement along the siphonal line to a marked extent together with the development of ventrolateral clavi or tubercles on the rib endings which change from an isometric arrangement across the venter (*Protohoplites*) to an en-echelon arrangement (*Otohoplites*). Ribbing may become effaced on the whorl flanks and, in *Otohoplites*, there is a marked tendency for ribs to join at the ventrolateral clavi to give a lautiform pattern, a feature which tends to accompany the trend in shell growth to produce the en-echelon arrangement of the ventrolateral clavi. Suture line typically hoplitid with deeply incised saddles and trifid lobes (Figs 43F–H).

DISCUSSION. The Subfamily Sonneratiinae is considered here to include the following genera and subgenera: *Sonneratia* Bayle 1878 (Type species *Ammonites dutempleanus* d'Orbigny and including as a synonym the subgenus *Eosonneratia* Savel'ev 1973*b* with type-species *Sonneratia*

(*Eosonneratia*) *vnigri* Savel'ev) with subgenus *Globosonneratia* Savel'ev 1973*b* (Type species *Sonneratia perinflata* Breistroffer); *Pseudosonneratia* Spath 1925*a* (Type species *Pseudosonneratia typica* Spath) with subgenus *Isohoplites* Casey 1954 (Type species *Parahoplites steinmanni* Jacob); *Tetrahoplites* Casey 1952 (Type species *Sonneratia subquadrata* Sinzow); *Protohoplites* Spath 1923 (Type species *Ammonites archiacianus* d'Orbigny) with subgenus *Hemisonneratia* Casey 1952 (Type species *Ammonites puzosianus* d'Orbigny); and *Otohoplites* Steinmann 1925 (Type species *Ammonites raulinianus* d'Orbigny). The interrelationships of these genera are shown diagrammatically in Fig. 44.

The Sonneratiinae, as interpreted here, is wholly of *mammillatum* Superzone age and is monophyletic with *Sonneratia* (*Globosonneratia*) as its earliest member. Its sutural pattern

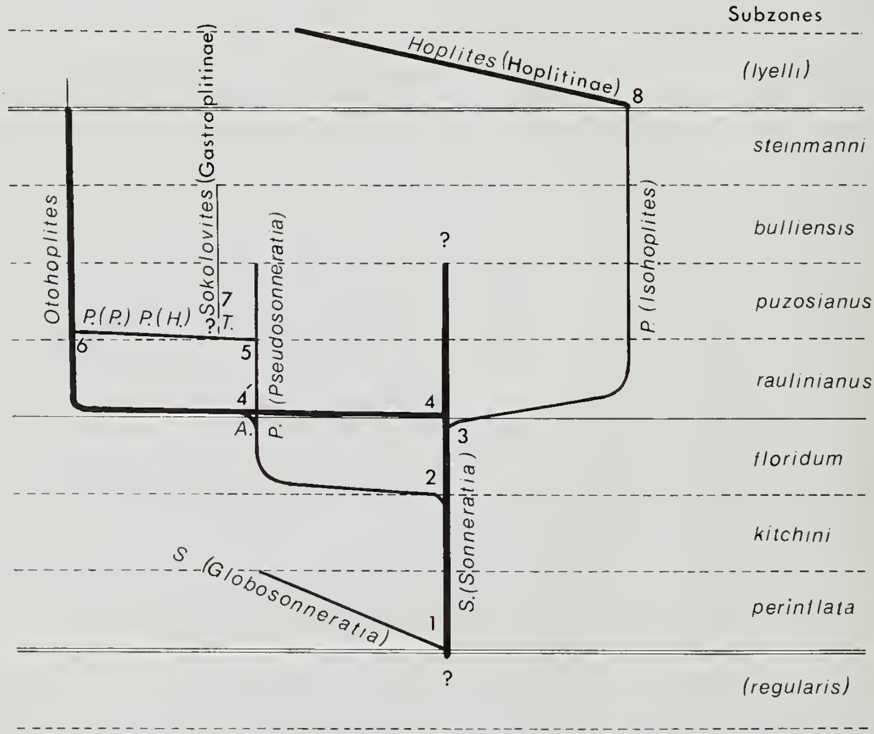


Fig. 44 Interrelationships of shell morphology in the various form genera and subgenera of the Sonneratiinae and their links with the Hoplitinae and Gastroplitinae.
A – Anahoplitoides, *T – Tetrahoplites*, *P.* (*P.*) – *Protohoplites* (*Protohoplites*), *P.* (*H.*) – *Protohoplites* (*Hemisonneratia*).
1. Development of globular shells.
2. Development of compressed forms with ribbing projected forward ventrally accompanied by some effacement along the siphonal line.
3. Development of compressed discoidal forms with strong projection of the ribbing forward onto the venter and a tendency to effacement along the siphonal line.
4. Total effacement of the ribbing along the siphonal line, lateral instability of the rib endings to form an en-echelon arrangement across the venter with tuberculation and lautiform ribbing. Depressed subquadrate forms from *Sonneratia*; laterally compressed forms from *Pseudosonneratia* via *Anahoplitoides* – 4′.

5–6. Secondary development of *Otohoplites* through *Tetrahoplites* – *Protohoplites* (*Hemisonneratia*) and *Protohoplites* (*Protohoplites*).

7. Probable development of *Sokolovites* from *Tetrahoplites* at the root of the Gastroplitinae.
8. Second phase of development of a stock analogous to *Otohoplites* from *Pseudosonneratia* (*Isohoplites*) to *Hoplites* by total effacement of the ribbing across the siphonal line and instability of the rib pattern to form en-echelon rib terminations across the venter.

suggests an origin in the desmoceratid subfamily Beaudanticeratinae (Figs 43F,G), probably within the genus *Uhligella*. Equally, the septal sutural pattern precludes a relationship with '*Farnhamia*' (i.e. *Arcthoplites*) despite the superficial similarity in the ornament which Casey (1954; 1960–) used as evidence of their genetic affinity.

The gross morphology of *Otohoplites* suggests a position within the subfamily Hoplitinae rather than in the Sonneratiinae. However, the origin of *Otohoplites* in *Pseudosonneratia* is independent of the later, end *mammillatum* Zone, development of *Hoplites*, *sensu stricto*, the earliest member of the Hoplitinae. This example of convergence is considered here to be an early experiment with only one species of *Otohoplites* surviving into the early Middle Albian (early *Lyelliceras lyelli* Subzone).

Genus ***SONNERATIA*** Bayle 1878

Subgenus ***GLOBOSONNERATIA*** Savel'ev 1973

TYPE SPECIES. *Sonneratia perinflata* Breistroffer 1947.

DISCUSSION. **(7).** *Sonneratia* (*Globosonneratia*) *globulosa* Savel'ev (1973*b*, pl. 24, figs 1a–c), the holotype of which is refigured here in Figs 16a–c, is used by Savel'ev as the index fossil of the basal Subzone of the *mammillatum* Superzone in Mangyschlak. The specimen is a nucleus closely comparable to those of *Sonneratia* (*Globosonneratia*) *perinflata* Breistroffer, an example of which is figured here in Figs 17a, b, and it is considered to be conspecific with Breistroffer's species. The large example named *Sonneratia coronatiformis* by Luppov (*in* Luppov *et al.* 1949) is also very close, if not conspecific, with *S.* (*G.*) *perinflata*.

Subgenus ***SONNERATIA*** *sensu stricto*

TYPE SPECIES. *Ammonites dutempleanus* d'Orbigny 1850.

DISCUSSION. **(8).** Savel'ev (1973*b*, 80) has recognized a subgenus *Eosonneratia* based upon *Sonneratia* (*Eosonneratia*) *vnigri* Savel'ev. A reproduction of the original figure of the holotype of *S.* (*E.*) *vnigri* is given here in Figs 23a, b for comparison with the example of *Sonneratia* (*Sonneratia*) *dutempleana* (d'Orbigny) figured in Figs 22a, b. In the writer's opinion, the subgenus *Eosonneratia* is not separable from *Sonneratia* (*Sonneratia*). The species *S.* (*S.*) *vnigri* is present in the *floridum* Subzone of western Europe (see Note 11 below).

(9). *Sonneratia* (*Eosonneratia*) *strigosa* Savel'ev (1973*b*, 83; pl. 23, figs 4a–c) and *Sonneratia daguini* Destombes (1979, pl. 4–11, figs 1–3) are considered here to be conspecific with *Sonneratia* (*Sonneratia*) *caperata* Casey (1960–, 537, 660; pl. LXXXVII, figs 2a, b) of *floridum* Subzone age. The original illustrations of the holotypes of *S. strigosa* and *S. daguini* are given here for comparison in Figs 18 and 19.

(10). The subspecies *Sonneratia ciryi compressa* Destombes (1979, pl. 4–10, figs 3a, b) is morphologically very close to the holotype of *Sonneratia* (*Eosonneratia*) *rotula* Savel'ev (1973*b*, 82; pl. 23, figs 3a–c) and it is considered here to be conspecific. The original illustrations of the holotypes are refigured here in Figs 20 and 21 for comparison.

(11). The holotype of *Sonneratia ciryi ciryi* Destombes (1979, pl. 4–10, figs 2a, b) is almost identical in appearance to that of *Sonneratia* (*Eosonneratia*) *vnigri* Savel'ev (1973*b*, 81; pl. 23, figs 2a, b) reproduced here in Figs 25 and 23 respectively. *S.* (*S.*) *vnigri* Savel'ev is present also in the condensed *floridum* and *raulinianus* Subzones pebble fauna of Bed 33 of Casey at Folkestone, Kent, under the name *Sonneratia* cf. *parenti* Jacob (Casey 1960–, pl. LXXXVII, figs 5a, b) refigured here in Figs 24a, b for comparison.

Genus ***PSEUDOSONNERATIA*** Spath 1925

TYPE SPECIES. *Pseudosonneratia typica* Spath 1925.

DISCUSSION. **(12).** *Pseudosonneratia typica* Spath is morphologically half way between the laterally compressed forms such as *P.* (*P.*) *palaeodentata* Destombes and *P. praedentata* Casey on the one hand, and the coarsely ribbed with subquadrate whorl section forms included in

Tetrahoplites, such as *T. subquadratus* Sinzow, on the other. Indeed, *Pseudosonneratia*, as interpreted at present, contains a number of forms transitional from *Sonneratia* to various specialized offshoots with hoplitinid-like characteristics and, at the end of the Lower Albian, to the subfamily Hoplitinae itself.

Within the *floridum* Subzone fauna of the Perchois Ouest quarry, Casey (1960–, 542, text-fig. 204) has described *Pseudosonneratia jacobi* and *P. crassa*, and Destombes (1979) has described *P. flexuosa* and *P. palaeodentata*, species which are not easy to separate generically from contemporary species of *Sonneratia* (*Sonneratia*) which occur in the same bed.

The genus *Otohoplites* Steinmann appears suddenly at the base of the succeeding *raulinianus* Subzone and, on first inspection, appears to be very different from the species of *Pseudosonneratia* referred to above. However, the differences are more apparent than real and there are rare transitions known between these two genera that are analogous to those between the *steinmanni* group of *Pseudosonneratia* (that is, *Isohoplites* Casey) and the genus *Hoplites* at the root of the subfamily Hoplitinae. It requires only a closely similar short-lived transitional phase to that of *P.* (*Isohoplites*) *steinmanni* (Jacob) and *P.* (*I.*) *laffrayei* Breistroffer to occur. This would involve further effacement of the ribbing across the venter with the ventrolateral rib endings terminating in clavate tubercles to produce a '*Protohoplites*' condition. As in the later, true *Protohoplites* of the *puzosianus* Subzone and in *Isohoplites* in the *steinmanni* Subzone, once the ribbing had been interrupted along the siphonal line, shell ornament growth became bilaterally unstable with the ribs becoming arranged en-echelon across the ventrodorsal axis of the shell. The intermediate stages between species of *Sonneratia* and *Pseudosonneratia*, such as *P. crassa* Casey, and early species of *Otohoplites* such as *O. raulinianus* (d'Orbigny) and *O. waltoni* Casey, are illustrated by forms such as *Sonneratia* (*S.*) *elegans* Casey (Figs 45a, b), the

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Figs 45–55 Transitions from *Sonneratia* and *Pseudosonneratia* to early *Otohoplites*. All illustrations × 1.

Figs 45a, b *Sonneratia* (*Sonneratia*) *elegans* Casey. Specimen showing a tendency for the ribbing to become effaced over the siphonal line. BGS Zq 52 R. Casey Coll., Bed 33, condensed *floridum* and *raulinianus* Subzones debris, Gault–Lower Greensand Junction Beds, near Copt Point, Folkestone, Kent.

Fig. 46 *Sonneratia* (*Sonneratia*) sp. Copy of the illustration by Destombes (1979, pl. 4–18, fig. 3) of the fragmentary specimen identified as *Protohoplites* (*Hemisonneratia*) *puzosianus* (d'Orbigny), Bed 2b, Perchois Est quarry, Aube, reduced to natural size.

Figs 47a, b *Sonneratia* (*Sonneratia*) sp., comparable form to that of Fig. 46 showing a similar instability of the rib pattern across the venter. BMNH C54300 L. F. Spath Coll. Same horizon and locality as Fig. 45.

Figs 48a, b *Sonneratia* (*Sonneratia*) sp., comparable form to that illustrated in Fig. 47. Copy of Destombes (1979, pl. 4–12, figs 2a, b) identified as *Protohoplites* (*Hemisonneratia*) *gallicus* Breistroffer, Bed 1c, Perchois Ouest quarry, Aube, reduced to natural size.

Figs 49a, b Early '*Protohoplites*' stage. Copy of the illustrations by Destombes (1979, pl. 4–13, figs 2a, b) identified as *P.* (*H.*) *gallicus*, Bed 1c, Perchois Ouest quarry, Aube, reduced to natural size.

Figs 50a, b Late '*Protohoplites*' stage. BMNH C79286 D. J. Ward Coll. Same horizon and locality as Fig. 45.

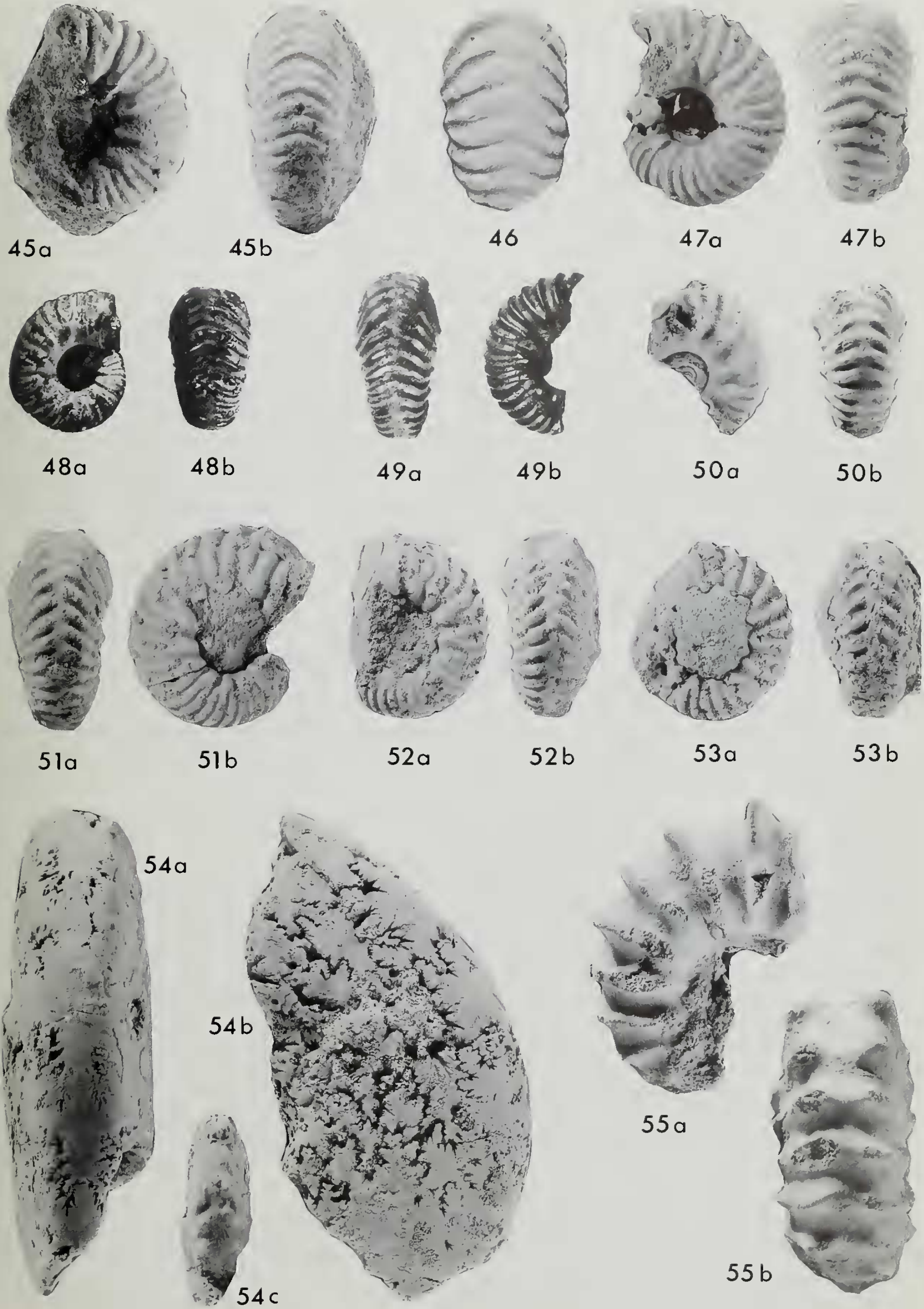
Figs 51a, b Nucleus of *Otohoplites waltoni* Casey showing the transition from a more continuous rib pattern across the venter to an en-echelon arrangement. BMNH C72265 Author's Coll. Same horizon and locality as Fig. 45.

Figs 52a, b Nucleus of the early form of *Otohoplites raulinianus* (d'Orbigny) BMNH C72387 Author's Coll. Same horizon and locality as Fig. 45.

Figs 53a, b A coarser ribbed nucleus of *O. waltoni* Casey. BMNH C90562 Author's Coll. Same horizon and locality as Fig. 45.

Figs 54a–c *Anahoplitoides* sp. a transitional form between *Pseudosonneratia* and *Otohoplites* of the *subguersanti–auritiformis* group. BGS Zn 9428 R. Casey Coll. Same horizon and locality as Fig. 45.

Figs 55a, b Body chamber fragment of a late '*Protohoplites*' stage of the same transitional form as that figured in Figs 50a, b, with modified *latisulcatus*-like single ribbing. BMNH C90282 C. W. & E. V. Wright Coll. Same horizon and locality as Fig. 45.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coarsely ribbed *P. crassa percrassa* Destombes (1979, pl. 4–8, figs 2a, b, 3a, b; pl. 4–9, fig. 2) from the *floridum* Subzone of the Perchois Ouest quarry; the nuclei figured by Destombes (1979, pl. 4–12, figs 2a, b, and pl. 4–13, figs 2a, b) as *Protohoplites* (*Hemisonneratia*) *gallicus* refigured here in natural size in Figs 48a, b, 49a, b; the specimens of '*Protohoplites*' figured here in Figs 50a, b, and 55a, b, the specimen of *Otohoplites waltoni* figured in Figs 51a, b, and the specimen of *O. raulinianus* figured in Figs 52a, b, the latter three specimens from the pebble fauna of Casey's Bed 33 (Bed 1a) at Folkestone, Kent, of mixed *floridum* and *raulinianus* age. Transitional forms between the discoidal forms of *Pseudosonneratia* (*Pseudosonneratia*) of the *floridum* Subzone and the flattened discoidal forms of early *Otohoplites* in the *raulinianus* Subzone, such as *O. guersanti* (d'Orbigny) and *O. auritiformis* (Spath), are provided by the specimens of *Anahoplitoides* which occur in the sediments of late *floridum* Subzone age in England and the Soviet Union (see Notes 17–18 opposite).

Similar transitions from *Pseudosonneratia* to *Otohoplites* occur again in the *puzosianus* Subzone where more than one series of shell forms can be traced from *Pseudosonneratia typica* Spath through *Tetrahoplites* to *Protohoplites*, and thence to *Otohoplites* by the same instability of shell growth leading to the en-echelon arrangement of ventrolateral rib endings seen earlier in the *raulinianus* Subzone and described above. It appears, therefore, that *Otohoplites* was produced in two waves, albeit that the second, *puzosianus* Subzone, wave was much reduced in numbers. Both originated in the earlier, more *Sonneratia*-like group of *Pseudosonneratia* to which the nominate subgenus is restricted here. The species of *Pseudosonneratia* in the *puzosianus* and *steinmanni* Subzones, which foreshadow *Hoplites* of the *dentatus* group, such as *P. acuta* Casey, *P. praedentata* Casey and *P. iserensis* Spath, group together naturally with *P. steinmanni* (Jacob) the type species of *Isohoplites* and are, therefore, now included in that subgenus, placed by Savel'ev (1976) and the writer (Owen 1985) in the genus *Pseudosonneratia* rather than in *Hoplites* (Casey 1954).

(13). The holotype of '*Hoplites* (*Isohoplites*) *eodentatus*' Casey (1961; B.G.S. GSM 98602) is now lost, but the original photographs of it show it to be conspecific with *Pseudosonneratia* (*Isohoplites*) *steinmanni* (Jacob). Amédro (1984*b*) has now formally redescribed this species. There are many transitions known between *P.* (*I.*) *steinmanni* and *Hoplites dentatus* (J. Sowerby) in which the ornament in individual specimens shows well the inherent instability between the isometric and en-echelon arrangements of the rib endings once the ornament across the siphonal line has become effaced.

Genus *OTOHOPLITES* Steinmann 1925

Type species. *Ammonites raulinianus* d'Orbigny 1841.

Discussion. The origin of *Otohoplites* from *Sonneratia* and *Pseudosonneratia* has been discussed briefly in the preceding section of this paper and under *Anahoplitoides* below. The genus persists into the early part of the *Lyelliceras lyelli* Subzone of the Middle Albian as a great rarity. Although *Hoplites*, like *Otohoplites*, manifests a tendency to a lautiform pattern of ribbing on the whorl flank, there is no evidence of a direct relationship between these two genera. Lautiform ribbing is considered here to be an advanced genetic character shared by the more specialized offshoots of both the Sonneratiinae and the Hoplitinae. Good examples of morphological convergence produced by this genetic character in forms not directly related is to be seen by comparing later species of *Otohoplites*, such as *O. subhilli* (Spath) of *bulliensis* Subzone age, with Middle Albian (*lautus* Zone) species of *Dimorphoplites tethydis* Spath *non* Bayle (e.g. Spath 1923–43, pl. XV, figs 1a, b), or of various species of *Otohoplites* with the Upper Albian *Callihoplites*.

(14). The holotype of *Otohoplites sinzowi* Savel'ev (1973*b*, 85–6; pl. 24, figs 4a–c reproduced here in Figs 38a–c) is considered to fall within the range of variation shown by *Otohoplites auritiformis* (Spath) (e.g. Figs 36, 37) with which it is now included.

(15). The holotype of *Otohoplites larcheri* Destombes (1979, pl. 4–22, figs 2a, b) and the first figured paratype (1979, pl. 4–18, fig. 4 and pl. 4–22, fig. 3) refigured here in Figs 14a, b fall within the range of morphological variation shown by *Otohoplites waltoni* Casey (Figs 15a, b). The second paratype of *O. larcheri* figured by Destombes (1979, pl. 4–22, figs 1a, b) refigured here in Figs 12a, b is closely comparable with the early form of *Otohoplites raulinianus* (d'Orbigny) figured by Casey (1960–, pl. LXXXIV, fig. 1) and refigured here in Figs 13a, b.

(16). The holotype of *Otohoplites venustus* Savel'ev (1973*b*, 87; pl. 25, figs 1a–c) is almost identifical to the holotype of *O. subhilli* (Spath) figured by Sinzow (1909, pl. II, figs 19, 20). *O. subhilli* is represented in the *bulliensis* Subzone sediments in the northern part of the Pays de Bray, France (e.g. the specimen figured by Destombes 1973, pl. 1, figs 3a, b), and in sediments of the same age in the Aube, France. The three figures referred to above are reproduced in Figs 26, 28, and 29 for comparative purposes.

Genus *ANAHOPLITOIDES* Casey 1961

Type species. *Saynella splendens* var. *gigas* Sinzow 1915.

Discussion. **(17 & 18).** The species upon which Casey recognized the genus *Anahoplitoides*, *A. gigas* (Sinzow), is represented by the unique holotype figured by Sinzow (1909, pl. 1, figs 1–4) from an uncertain subzonal position within the *mammillatum* Superzone deposits of Mangyschlak, Soviet Union. A similar form with straighter ribs was found in the *floridum* Subzone sediments in Surrey (Casey 1960–, 548, 549, text-fig. 208e, f). Casey considered this species to be a forerunner of the Middle and Upper Albian genus *Anahoplites*, the link being the ammonite described by Spath (1923–43, 131; pl. XI, figs 7a, b) as *Anahoplites mimeticus* and said to have come from the Carstone of Niton, Isle of Wight. Casey also figured an example of '*Anahoplites mimeticus*' (C. W. & E. V. Wright Coll. No. 9983, BMNH C84769) alleged to have come from the top of the Carstone (*eodentatus*—i.e. *steinmanni* Subzone) of Bonchurch, Isle of Wight (Casey 1960–, 547, text-figs 207a, b). It is necessary to repeat the observation made previously by the author (Owen 1971, 47) that neither Spath's holotype of *A. mimeticus*, nor the specimen figured by Casey, are preserved in a manner indicating derivation from the Carstone. Kennedy & Hancock (1978, v6) have more recently listed the occurrence of this species in the *eodentatus* Subzone, but this is an error. The preservation of the specimens mentioned above is that of the Gault clay and both were found loose. Spath's holotype of *A. mimeticus* is a late *spathi* Subzone specimen of *Hoplites* with coarse inner whorls and a relatively smooth outer whorl. Casey's specimen is an early form of *Anahoplites* of the *intermedius* Subzone.

Anahoplitoides gigas (Sinzow) is considered here to be a short-lived transitional form between *Pseudosonneratia* and compressed species of *Otohoplites* referred to earlier (pp. 220, 222), other transitions of which are known to occur at the end of *floridum* Subzone times. The ribbing shows the relatively simple pattern of a compressed, discoidal species of *Pseudosonneratia*, such as *P. palaeodentata* Destombes, with a venter upon which the ribbing has become effaced along the siphonal line. This stage corresponds to the later, *steinmanni* Subzone, transitions between *Pseudosonneratia* (*Isohoplites*) and *Hoplites* discussed above (p. 222). On this analogue, *A. gigas* is transitional to the compressed, discoidal forms of *Otohoplites* in the *raulinianus* Subzone, such as *O. subguersanti* Casey, *O. guersanti* (d'Orbigny) and *O. auritiformis* (Spath), in which the ventrolateral rib-endings have developed into clavi that have commenced to adopt an en-echelon arrangement across the venter, and in which lautiform ribbing has become apparent. The adult whorl of *A. gigas* is distinctly like that of *Otohoplites*. A similar, although coarser-ribbed, transition of this type is provided by BGS Zn 9428 (R. Casey Coll.) from the mixed *floridum* and *raulinianus* debris of Bed 1a (Casey's Bed 33) at Folkestone, Kent, figured here in Figs 54a–c, in which the ribs are still arranged isometrically each side of an effaced siphonal line.

Subfamily **GASTROPLITINAE** Wright 1952

Diagnosis. Moderately involute discoidal to robust shells with flattened sides and narrowly arched rounded to tabulate venters. Ribs blunt, gently biconcave to curved, regularly bifurcating from comma-shaped bullae close to the umbilical margin. Ribs continuous across the venter, showing slight forward projection only along the siphonal line, but with a tendency to an en-echelon arrangement in forms in which the ribs are effaced, or reduced, as they cross the siphonal line. In later genera, the ribs develop clavate tubercles at the ventrolateral shoulders and eventually along the siphonal line. The septal sutural configuration shows a broad first lateral saddle, deeply indented trifid first lateral lobe and relatively simple auxillary saddles and lobes (Figs 43J–K).

Discussion. **(19).** The earliest members of the Gastroplitinae are of *mammillatum* Superzone age. However, the Subfamily reaches its known acme in the Upper Albian and, possibly, in the lower Cenomanian within the Arctic faunal province. It is included here in the Hoplitidae rather than in the Cleoniceratidae for the following reasons. The two earliest forms, the European and Arctic provinces genus *Sokolovites* and '*Anahoplites*' *yakounensis* (Whiteaves) of the north Pacific province, show close affinities with discoidal species of *Tetrahoplites*, a genus included in the Sonneratiinae. Their origin lies, therefore, within the Sonneratiinae which in turn is derived from a beudanticeratinid ancestor (Fig. 44). The Cleoniceratidae on the other hand has its origin within the Puzosiinae. In the Gastroplitinae, the development and plan of the rib ornament differs significantly from that of the Cleoniceratidae and is akin to that of the Sonneratiinae. Moreover, this pattern tends to run parallel to that of the Hoplitinae. The septal sutural pattern does not show the marked asymmetry of the first lateral lobe characteristic of the Cleoniceratidae and is essentially hoplitid in its configuration (Figs 43J–K).

The following genera are included here in the Gastroplitinae: *Sokolovites* Casey 1966 (Type species *Sokolovites subdragunovi* Casey and including, as a synonym, *Cleogastroplites* Jeletzky 1980 with type species *Cleogastroplites aberrans* Jeletzky); *Pseudopulchellia* Imlay 1961 (Type species *Pseudopulchellia pattoni* Imlay and including as a synonym *Stelckiceras* Jeletzky 1980 with type species *Placenticeras perezianum*? var. *liardense* Whiteaves); *Gastroplites* McLearn 1930 (Type species *Hoplites canadensis* Whiteaves and including as synonyms *Stotticeras* Jeletzky 1980 with type species *Stotticeras crowense* Jeletzky and *Pseudogastroplites* Jeletzky 1980 with type species *Pseudogastroplites arcticus* Jeletzky); *Neogastroplites* McLearn 1930 (Type species *Buchiceras*? *cornutum* Whiteaves).

Superfamily **ACANTHOCERATACEAE** de Grossouvre 1894

Family **LYELLICERATIDAE** Spath 1921

Discussion. The family Lyelliceratidae is considered here to include two subfamilies, the Leymeriellinae Breistroffer 1952 and the Lyelliceratinae *sensu stricto*.

Subfamily **LYELLICERATINAE** Spath 1921

Discussion. **(20).** The genus *Tegoceras* Hyatt has its earliest known occurrence in the *Cleoniceras floridum* Subzone and then persists throughout the remainder of the Lower Albian. Although there is some resemblance to the earlier subfamily Leymeriellinae (e.g. *Leymeriella* (*Neoleymeriella*) *consueta* Casey), a phylogenetic link has still to be established during the earlier part of the *chalensis* Zone. However, the change in form from that of *Tegoceras* to that of *Lyelliceras* has long been recognized and described in some detail (e.g. Spath 1923–43, 313; Owen 1971, 120; Destombes, Juignet & Rioult 1973; Casey 1960–, 622–7). *Tegoceras* passes through a short-lived transitional phase at the end of the *steinmanni* Subzone into *Lyelliceras* which is characteristic of the basal Middle Albian. In this respect, the transition parallels that of the contemporaneous change in the Hoplitidae from *Pseudosonneratia* (*Isohoplites*) spp. into *Hoplites*. In the case of *Tegoceras*, the ribbing becomes sharper with the development of lateral and siphonal rows of tubercles like those of *Lyelliceras*, but the ribbing retains the typical zigzag pattern over the venter characteristic of *Tegoceras*. These transitional forms include *Lyelliceras pseudolyelli* (Parona & Bonarelli), *L. hirsutum* (Parona & Bonarelli) and *L. huberianum* (Pictet) among others (Owen 1971; Destombes, Juignet & Rioult 1973).

Casey (1960–, 624) regarded the geographical distribution of *Tegoceras* as being essentially European. This is untrue, however, and reflects the fact that *mammillatum* Superzone sediments are only patchily preserved within the Tethyan region. Typically, the known geographical distribution of *Tegoceras* extends within the Tethyan and Gondwanan province from Venezuela (Renz 1982, 39; pl. 5, figs 16a, b) to Madagascar (Collignon 1963, 317, fig. 1346), and the transitional forms to *Lyelliceras* at the junction of the equivalent of the European province *steinmanni* Subzone are equally as widespread. Like its even more widely distributed descendant *Lyelliceras* (which includes '*Prolyelliceras*'—see Owen 1971, 135) of the basal Middle Albian, *lyelli* Subzone, the incursions of *Tegoceras* into the European shelf seas were limited to the Anglo-Paris Basin and the southern marginal regions of the hoplitinid faunal province. *Tegoceras* is important, therefore, in the inter-provincial correlation of later *mammillatum* Superzone sequences.

Family **MOJSISOVICSIIDAE** Hyatt 1903

DISCUSSION. **(21).** The Mojsisovicsiidae is considered here to comprise only the subfamilies Mojsisovicsiinae *sensu stricto* and Mortoniceratinae Spath 1925*b*. The origin of the family remains as obscure as when Casey (1960–, 630–2) described its earliest known member, *Oxytropidoceras alticarinatum* (Spath), which is known in England from the mixed phosphatic debris of *floridum* and *raulinianus* Subzones age in Bed 33 of Casey (Bed 1a) at Folkestone, Kent.

Casey (1957, 38) envisaged an origin of this family, along with the Leymeriellinae, Lyelliceratinae and Brancoceratidae, in the puzosiinid genus *Callizoniceras* during the *tardefurcata* Zone. A puzosiinid ancestry is established for the Leymeriellinae in *Callizoniceras* (*Wollemanniceras*) in the late Aptian and earliest Albian (Brinkmann 1937), and for the Brancoceratidae in *Silesitoides* (p. 226) within the later part of the *mammillatum* Superzone. However, the origin of the families Lyelliceratidae and Mojsisovicsiidae advocated here differs from the opinion given by Casey.

A possible origin of *Tegoceras*, the earliest recognized lyelliceratid, in evolute coarsely ornamented species of *Leymeriella* has been mentioned above (p. 224). In the case of the Mojsisovicsiidae, the ribbing seen in species of *Oxytropidoceras* within the early Middle Albian is also similar to that of the less robustly ornamented, discoidal species of *Leymeriella* such as *L. renascens* Seitz. As Casey has pointed out, the tendency among ammonite lineages is to produce oxyconic end forms. The possibility that the Mojsisovicsiidae represent a successful and long-lived oxyconic development of later *tardefurcata* Zone discoidal species of *Leymeriella* should not be discounted. The Mojsisovicsiinae and its descendants, the Mortoniceratinae, cannot be considered a collection of keeled end stocks but represent a morphologically evolving group of considerable diversity throughout the Middle and Upper Albian for which separation at family rank is justified.

The only other known species of *Oxytropidoceras* of *mammillatum* Superzone age is *O. packardi* Anderson from the basal part of the Packard Member ('Zone' of Anderson 1938) of the Hulen Formation (Horsetown Group) in the Sacremento region of the Californian Pacific coastal region. The relatively wide geographical separation of the Californian and European areas in Albian times, despite their closer proximity, points to an early history of development of the Mojsisovicsiinae within the Tethyan region despite their possible European province ancestry in *Leymeriella*. Differentiation of this stock continued in the Tethyan region during the Middle Albian.

Family **BRANCOCERATIDAE** Spath 1933

DISCUSSION. **(22).** The family Brancoceratidae Spath formerly encompassed a group of three subfamilies whose origins, albeit that they are still unclear, were sufficiently known to render the family polyphyletic. In the *Treatise* (Wright *in* Arkell *et al.* 1957, L402–9), it is inferred that the Brancoceratinae *senso alto* and the Mojsisovicsiinae had a common origin in the Desmocerataceae, perhaps from *Silesitoides* or a closely allied genus. The genus *Silesitoides* Spath 1925 (Type species *Silesites escragnollensis* Jacob) has a known age range in the extreme southern border region of the European province from the *Leymeriella regularis* Subzone (*tardefurcata*

Zone), through the *mammillatum* Superzone and into the early Middle Albian *Lyelliceras lyelli* Subzone. It is known to have given rise to the genus *Parabrancoceras* Breistroffer 1952 (Type species *Brancoceras besairiei* Collignon) in the *mammillatum* Superzone, the earliest known member of the Brancoceratidae as restricted here. Indeed, *Parabrancoceras besairiei* (Collignon) found in late *mammillatum* Superzone sediments in Madagascar is scarcely separable generically from a contemporary species of *Silesitoides* (e.g. BMNH C51695), a member of the Subfamily Puzosiinae. *Parabrancoceras* is now known from sediments of *steinmanni* Subzone age as far north as Maurupt, Marne, on the south-eastern margin of the Paris Basin (recorded as *Brancoceras* sp. by Owen 1971, 89). It is well represented in the condensed *steinmanni* to late *spathi* Subzone debris in the lower part of the sequence in the vicinity of Escragnolles, Alpes Maritimes, France, and it can be inferred from transitional forms between *Parabrancoceras* and *Brancoceras* that the family stems from a common ancestor. The derivation of this family from *Silesitoides* is very far from what is known at present of the origin of the Mojsisovicsiidae.

The family Brancoceratidae is restricted here to the nominate subfamily, with the exclusion, therefore, of the Mojsisovicsiinae and its descendants grouped as the Mortoniceratinae. As such, the family is monophyletic with a common puzosiinid ancestor. The detailed development of the Brancoceratidae and Mojsisovicsiidae can only be elucidated from suitable Tethyan province sequences, the short-lived invasions at intervals into the European shelf seas being insufficient to give a detailed picture. Unfortunately, the stratigraphic record of the *mammillatum* Superzone in the Tethyan–Gondwanan shelf seas is very scattered and incomplete and virtually nothing is known of the oceanic sequences. The exact relationship between *Brancoceras* and *Eubrancoceras* for example has still to be determined. In some respects, *Eubrancoceras* is convergent to the Lyelliceratidae, suggesting a close relationship. However, this convergence probably reflects an ultimate origin of Lyelliceratidae and Brancoceratidae within the Puzosiinae, albeit from widely separated genera.

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